Chadronian “Insectivores” of the Cypress Hills, Saskatchewan

A thesis submitted to the College

of Graduate Studies and Research

in partial fulfilment of the requirements

for the degree of Master of Science

in the Department of Geological Sciences

University of Saskatchewan

Saskatoon

by

Taran Meyer

Permission to Use

In presenting this thesis in partial fulfilment of the requirements for a Master's degree from the University of Saskatchewan, I agree that the libraries of the University of Saskatchewan may make it freely available for inspection. I further agree that permission for copying of this thesis in any manner, in whole or in part, for scholarly purposes may be granted by the professors who supervised my thesis work or, in their absence, by the Head of the Department of Geological Sciences or the Dean of the College of Graduate Studies and Research. It is understood that any copying or publications or use of this thesis or parts thereof for financial gain shall not be allowed without my written permission. It is also understood that due recognition shall be given to me and to the University of Saskatchewan in any scholarly use which may be made of any materials in my thesis.

Requests for permission to copy or to make other use of material in this thesis in whole or part should be addressed to:

Head of the Department of Geological Sciences

114 Science Place

University of Saskatchewan

Saskatoon, Saskatchewan S7N 5E2

Acknowledgments

The greatest thanks go out to my supervisor, Dr. Harold N. Bryant, who introduced me to little teeth in the dirt and the stories they can tell.

For financial support I thank NSERC, the University of Saskatchewan, and the Government of Saskatchewan .

I would like to thank the Royal Saskatchewan Museum and Royal Ontario Museum for use of their collections from the Cypress Hills, and also the American Museum of Natural History, the Carnegie Museum, the Field Museum, and the National Museum of Natural History (Smithsonian) for the invaluable loan of comparative materials.

Thank you, Dr. Ernie Walker, for the use of your lab and camera for my photography; thanks also to the rest of my committee. Thanks also go out to Frank McDougall, for sharing your thoughts, ideas, and diagrams regarding the Horse Locality and to Dr. Allen Kihm for your information concerning the Medicine Pole Local Fauna and also for valuable discussion. I would also like to thank the Geological Sciences secretaries, Jane Ritz and Brenda Britton, for all their help in too many areas to count.

On a personal level, I wish to thank all my friends and relatives who have been there, offering support (and childcare!) when the crunches came. Most especially my husband, Robin; this would have been impossible without you. Also my sister-in-law, Danielle Peters, and my neighbour Cathy Coutu, for stepping in to help look after my children in this last busy stretch.

Abstract

The Cypress Hills Formation of Saskatchewan preserves sediments of Uintan (middle Eocene) to Hemingfordian (middle Miocene) age, but the best-represented period is the Chadronian North American Land Mammal Age. The best-known site, with the richest biodiversity known for the area, is the middle Chadronian Calf Creek Locality, from which over 70 mammal and 25 non-mammal species are known. The majority of these taxa have been described in the literature, but the portion of the fauna which includes the "insectivores," members of the orders Leptictida, Apatotheria, and Lipotyphla, have not been formally described.

The following thesis identifies and describes the insectivores and chiropterans of the Calf Creek Locality, together with the same groups from the nearby Chadronian-aged Horse Locality. The inclusion of the Horse Locality specimens serves three purposes: (1) to begin the formal description of material from the Horse Locality, (2) to compare the two faunas to identify possible differences between the two, and (3) to allow for analysis of the implications of any faunal differences in terms of age and environment of the two sites.

The insectivore faunas of the two sites are found to be very similar, with the same genera and common species occurring at both localities. Six species-level differences are reported, all within relatively rare taxa; in most cases rare taxa were found at the Calf Creek but not at the Horse Locality. It seems likely that most of the specific differences result from the smaller collection size of the Horse Locality rather than from age-related species turnover. Although the non-insectivore taxa suggest that the Horse Locality dates from either later in the middle Chadronian or the Late Chadronian, an evolutionary change between the Calf Creek and the Horse localities could not be confirmed in the groups studied here.

Chadronian "Insectivores" of the Cypress Hills, Saskatchewan
Table of Contents

List of Tables

List of Figures

List of Plates:

Acronyms:

RSM, Royal Saskatchewan Museum; ROM, Royal Ontario Museum; AMNH, American Museum of Natural History; CM, Carnegie Museum; FM, Field Museum; CMNH, Chicago Museum of Natural History; USNM, United States National Museum (Smithsonian); CC, Calf Creek Locality; H, Horse Locality; AP, anteroposterior; BL, buccolingual; LAH, length at hypocone (see Fig. 2.4), LBH, length buccal to hypocone (see Fig. 2.4); LOT, length of trigonid (see Fig. 2.4).

Chapter 1

Introduction

By the end of the Eocene, 34 million years ago, the dinosaurs were long gone and mammals had proliferated, becoming the dominant element of terrestrial vertebrate fossil faunas throughout the world. Although many archaic mammalian groups persisted, the early ancestors of our modern orders of mammals had also appeared, laying the groundwork for our modern ecosystem. Even- and odd-toed ungulates, such as the ancestors of today's camels, horses, and rhinoceroses, browsed the forests of North America before the spread of the first grasslands alongside the gigantic brontotheres and fierce-looking entelodonts. Carnivores, including early relatives of dogs and cats, hunted in competition with the dominant creodonts, and a host of other creatures familiar and strange roamed the open woodlands of central North America. Beneath the feet of this majestic megafauna scurried a diverse collection of small mammals, including the first rodents, rabbits, and early relatives of shrews and hedgehogs, alongside a bevy of peculiar archaic forms.

Of course we know of these beasts, at once fabulous and familiar, only from the fossils they have left behind; the ancient river- and lakebeds of North America are encrusted with their remains, exposed wherever modern erosion has cut into the ancient sediment. Their bones tell us the stories of their myriad adaptations, from the primitive clawed, multi-toed mammalian archetype into a host of diverse forms with as many functions; but the bones tell only a part of the story. Vertebrate teeth, with their tough enamel, are among the most durable and recognizable elements of the terrestrial fossil record. In the case of the morphologically complex and intricately-occluding teeth of mammals, the dentition is not only the most durable part of the

skeleton, it is highly informative in terms of diet and lifestyle, and, perhaps most critically, one of the most diagnostic in the recognition of fossil species. Thus even the most battered, disarticulated and fragmented of mammalian fossil faunas can yield a rich and detailed portrait of the ancient world, and accumulations of small, fragmentary remains can rival or surpass the importance of more complete, but isolated, finds, in their ability to tell us about the communities these animals inhabited.

Put together, the durability, distinctiveness, and rapid evolution of mammalian teeth also make them ideal biostratigraphic markers. Where the fossils and their stratigraphy are well understood, the age of a fossil site can sometimes be determined to within a million year or less. In North America the terrestrial fossil record has been divided into ages based solely on mammalian fossils, and these North American Land Mammal Ages are the primary biostratigraphic units in use by students of North American Cenozoic palaeontology.

The majority of Tertiary mammal fossils in North America have been recovered from geologic formations in the American mid-west, particularly the states of Montana, Wyoming, South Dakota, and Nebraska, particularly those from the beds of the famous White River Group. Other fossil sources are known from the western states, including the John Day Formation of Orgeon, and also to the south, such as the Vieja Group of Texas. The formation most abundant in Tertiary mammal fossils north of the 49th parallel is the Cypress Hills Formation of southwest Saskatchewan. Its faunas provide a unique glimpse of the animals which occupied the northern plains from the middle Eocene to the middle Miocene, between 45 and 15 million years ago, and their similarities to and differences from their more southern relatives.

The late Eocene Calf Creek Local Fauna is the most prolific, best-known and best-studied fossil fauna in the Cypress Hills Formation of Saskatchewan, and has been the subject of study

for over eighty years. Most of the major elements of the fauna were thoroughly published by the mid 1980s, but considerable work remained to be done on members of the "insectivore" groups: leptictids, lipotyphlans, and apatotherians. Preliminary identifications of these taxa were begun by Loris Russell in the 1960s and 70s and continued by John Storer in the 1980s and 90s, but detailed and comprehensive examination had never taken place, and the published literature of several of these groups has been revised significantly since the last published descriptions of Russell (1972). The following thesis represents this examination, providing a comprehensive picture of the "insectivore" portion of the Calf Creek Local Fauna.

Although the best-studied, the Calf Creek Locality is not the only rich fauna of its age in the Cypress Hills. A large collection has also been amassed from the Horse Locality, a nearby site of similar faunal richness. Preliminary examination of taxa from the Horse Locality suggested an age very similar to the Calf Creek, but perhaps a little younger. Examination of the "insectivores" from this locality was undertaken with the intention of comparing them with similar taxa from the Calf Creek to assess faunal change in these groups over a geologically short span of time.

Since "insectivores" are not commonly used in biochronology and faunal correlation, the ability to demonstrate change over such a brief period could indicate an overlooked tool for the correlation of fossil mammal localities, and add resolution to the record of species change which is the basis for North American mammal biochronology. At the same time, a better understanding of the morphology and taxonomy of fossil insectivores brings us one step closer to understanding the history of this troubled group.

Figure 2.1— Southwestern Saskatchewan, southeastern Alberta, and northern Montana, showing Cypress Hills and probable source areas for sediment (Sweetgrass Hills, Bearpaw Mtns, Highwood Mts). Black rectangle indicates area of Fig. 1.3. Map from MSN Encarta, http://encarta.msn.com/encnet/features/mapcenter/map.aspx

Chapter 2

The Cypress Hills Region

i. Geology

The Cypress Hills Region is an elevated area of southwestern Saskatchewan and southeastern Alberta with a distinct ecology and geological history (Fig. 2.1). It represents the highest point of elevation in Canada east of the Rocky Mountains, and was the only part of Saskatchewan not completely buried by Pleistocene glaciation. It also forms the divide between the north-east draining basins of the Saskatchewan Rivers and the south draining Missouri-Mississippi River basin (Martz & de Boer, 1999). It preserves deposits ranging in age from the middle Eocene to middle Miocene, an interval poorly represented elsewhere in the country.

Although currently limited in extent, the formation represents the remnants of deposition which probably once covered extensive portions of Saskatchewan, Alberta, and Montana (Williams and Dyer, 1930; McDougall 1995).

The Cypress Hills Formation consists of terrigenous sediments ranging in texture from boulders through to silts and clays, largely unconsolidated. It unconformably overlies the Bearpaw (Late Cretaceous) and Ravenscrag (Paleocene) formations (Vonhof, 1965). Furnival (1946) estimated the thickness of the formation at about 167 m, while Vonhof (1965) estimated an average thickness of only 40 m, with a maximum thickness of about 76 m. Vonhof attributed Furnival's greater thickness to the inclusion of reworked Cypress Hills sediment in lower stratigraphic situations. Nevertheless, McDougall (1995) measured up to 190 m of in situ formation in some locations.

The sediment is fluvial. Channel-cuts, cross-bedding, and imbricated gravels indicate the presence of swift-flowing streams, while beds of finer laminar sedimentation represent overbank deposition in interchannel ponds (Vonhof, 1965; Leckie and Cheel, 1989). The poorly sorted mixtures of clay pellets, sands, and gravels that often produce fragmentary fossils are interpreted as debris-flows (Leckie and Cheel, 1989). Individual beds are highly variable and change rapidly laterally as well as vertically. Correlation over even moderate distances has generally been considered impossible (Vonhof, 1965), although McDougall (1995) (Fig. 2.2) identifies some large-scale features that appear consistently, including the basal cobble conglomerate and a silt/clay layer overlying the Calf Creek locality but below the Horse locality. The source of the

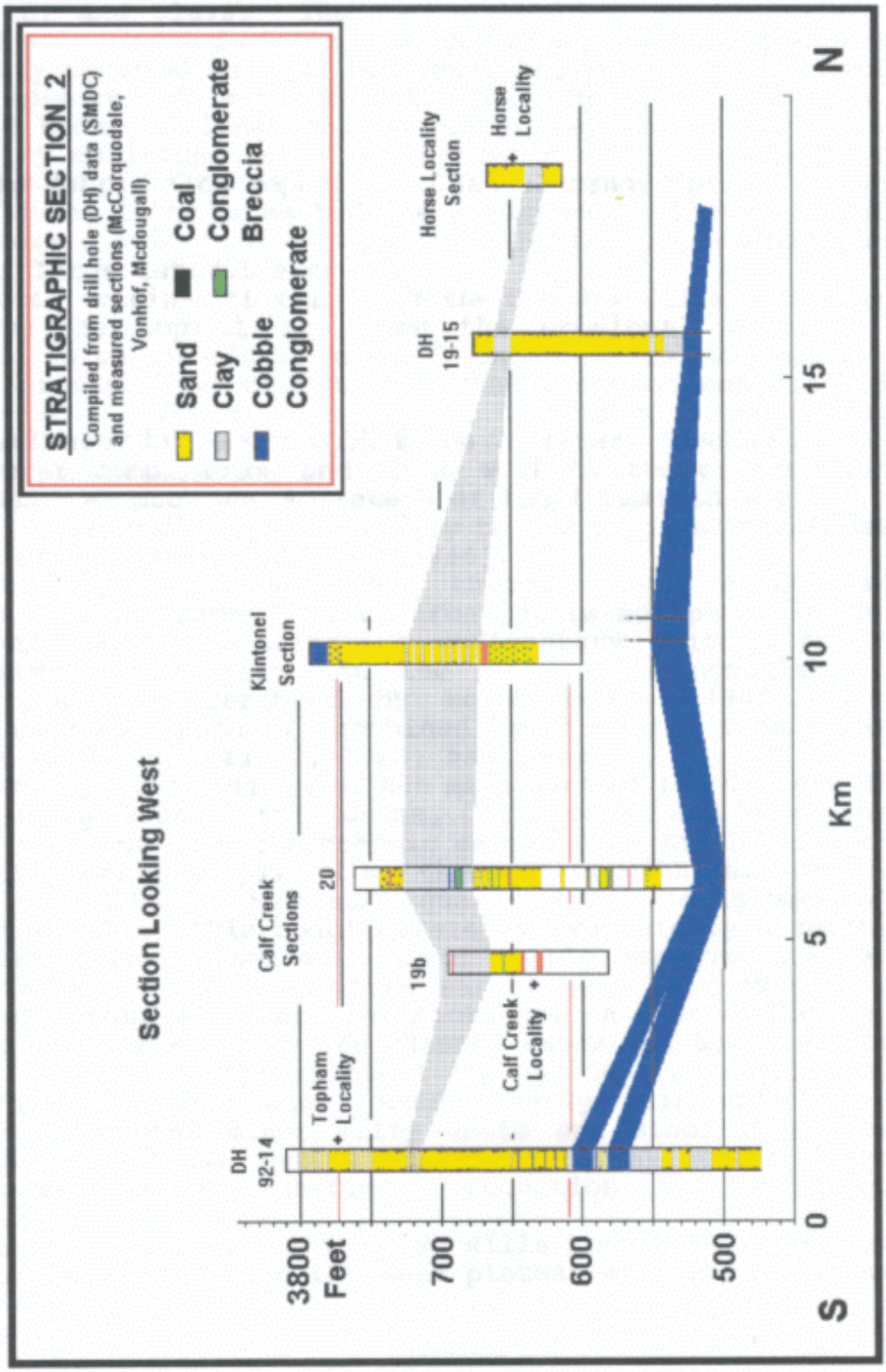


Figure 2.2— general correlation of stratigraphic sections from across the Cypress Hills. Relative positions of the Calf Creek and Horse local faunas are shown. Section 19b is derived from the same sections, measured by B. A. McCorquodale, as the Calf Creek screening locality section illustrated in Fig. 3.2. From McDougall, 1995.

sedimentary material has generally been identified as the Rocky Mountains to the west or southwest (eg. Russell, 1972), particularly the Highwood and Bearpaw Mountains and Sweetgrass Hills of northwest Montana (Fig. 2.1) (Vonhof 1965, Leckie and Cheel, 1989). Only Williams and Dyer (1930) reported pebble imbrications indicating a flow to the south.

In the model of Leckie and Cheel (1989), torrential precipitation in the sediment source regions produced flash-flooding and periods of extremely high flow rates, accounting for the presence of boulders and gravels (especially in the western Cypress Hills) at such a large distance from the source area. McDougall (1995) argued that the thick layer of basal conglomerate throughout the area (Fig. 2.2) was the result of a massive change in drainage systems caused by the formation of the Sweetgrass Hills and Bearpaw Mountains, and suggested that many of the later, generally finer, conglomerates were reworked from this material.

Table 2.1—Studies on the Palaeontology of the Cypress Hills region:

Bell (2004)
Bryant (1991, 1992, 1993)
Cope (1885a &b, 1889a & b, 1891)
Eberle and Storer (1995)
Holman (1963, 1968, 1972)
Krishtalka et. al. (1982)
Lambe (1905a, 1905b, 1905c, 1908)
Lundberg (1975)
Meyer (2002)
Rothecker (2003)
Russell (1934, 1936, 1938, 1940, 1965, 1972, 1975, 1976, 1978, 1980a & b, 1982, 1984)
Russell and Wickenden (1933)
Skwara (1986, 1988)
Sternberg (1924)
Storer (1975a & b, 1976, 1978, 1981a & b, 1983, 1984a & b, 1987, 1990, 1992, 1993a & b, 1994, 1995, 1996, 2002)
Storer and Bryant (1993, 1997)
Weigel (1963)
Williams and Storer (1998).

ii. History of Study in the Region

Tables 2.1 and 2.2 list studies on the palaeontology and geology, respectively, of the Cypress Hills region. The geology of the Cypress Hills was first studied by G. M. Dawson in 1874, who authored a report on the region for the British North American Boundary Comission in 1875. R. G. McConnell (1885) continued explorations, producing the first vertebrate fossils, which were described by E.

D. Cope (1885a & b).

L. M. Lambe collected and studied the fossils of the region, particularly from the Bone Coulee area (see Fig. 1.3), in the early 1900s (Lambe 1905a,b,c; 1908).

Table 2.2—Studies on the geology of the Cypress Hills Formaion

Dawson, (1875)
Davis (1918)
Furnival (1946)
Kupsch (1956)
Leckie and Cheel (1989, 1990)
McConnell (1885)
McDougall (1995)
McLearn (1928)
Nurkowski (1984)
Russell (1950, 1957)
Weston (1894)
Williams and Dyer (1930),
Vonhof (1965, 1969)

The formal term "Cypress Hills Formation" was first used by Williams and Dyer (1930). In 1933 Russell and Wickenden coined the term "Swift Current beds," later emended to "Swift Current Creek beds" (Russell, 1950), for Eocene deposits in the Swift Current area, but there is no lithological distinction between the two units, and the older beds are now included within the term Cypress Hills Formation (Storer, 1996).

Loris Russell authored many publications on the geology and palaeontology of the Cypress Hills between 1933 and the early 80s. In the 1960s Jan Vonhof pursued master's and doctoral work on the sedimentology of the Cypress Hills Formation. Bruce McCorquodale of the Royal Saskatchewan Museum was also active during this period, measuring many sections throughout the Cypress Hills (see Fig. 2.2, 3.1) and collecting fossils from various localities, but his findings were never published. In the 1970s a shift began from describing the composite fauna of the Formation as a whole to describing more limited faunas from one or two localities (Holman, 1972; Storer, 1975a, 1978). The work of Leckie and Cheel (1987, 1989) represents the most recent published studies on the sedimentology of the region, although McDougall has undertaken considerable unpublished work. The 1980s and 90s were characterized by the description of a number of local faunas representing different time periods within the deposition

of the Formation.

iii. Age of the Formation

The standard timescale reference system for North American Cenozoic mammalian biochronology is the North American Land Mammal Ages (NALMA) (Fig. 2.4) first codified by the Wood Committee in 1941. Nineteen ages were named and defined based on type sections and characterized by genus-level faunal lists. Although many ages were named after geologic units, the intent was to describe time units distinguished by fossil content alone (Wood et al, 1941). Since their initial publication, adjustments to the correlations have been made as necessary (e.g. Prothero and Swisher, 1992) when new faunal, palynological, or magnetostratigraphic information has illuminated problems with the original definitions; the ability to subdivide the NALMAs has also increased. The adjustment of most concern to this project represents a change in the correlation of NALMAs to the European epochs. In the original scheme, the Chadronian age was considered Early Oligocene. However, with refinements and adjustments to the age of both the Eocene/Oligocene boundary and the Chadronian/Orellan boundary, the Chadronian is now considered to fall within the Eocene. The

Figure 2.3—detail of western Cypress Hills showing localities mentioned in text. Two lines in the Calf Creek Locality circle indicate the sections measured by Mcorquodale.

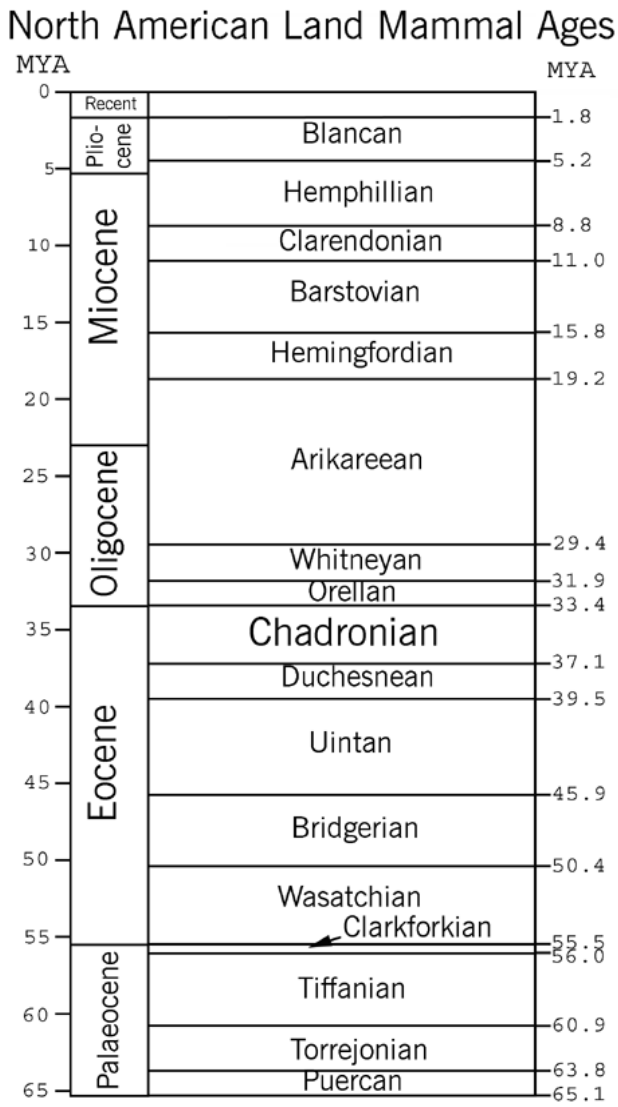


Figure 2.4—North American Land Mammal Ages. Based on Prothero (1998).

Chadronian/Orellan boundary now approximates the Eocene/Oligocene boundary, at about 34 mya (Prothero and Swisher 1992).

During the 1800s, the Cypress Hills Formation was judged to be of roughly the same age as the highly fossiliferous White River Group of the American Midwest (Cope, 1885a & b, 1889a & b, 1891), which was considered Oligocene. McConnell (1885) labeled the Cypress Hills Formation as Miocene, and Weston (1894) followed him, but their usage of "Miocene" likely included the Oligocene (Williams and Dyer, 1930). Matthew (1903), in his publication of the Pipestone Springs Fauna, observed greater similarity between the published Cypress Hills material and the fauna of the "*Titanotherium* beds" of the White River, the period that would later be known as the Chadronian.

Based on the fossil horses in his collection, Lambe (1905b, 1908), expressed the opinion that the Cypress Hills beds preserved material of the same age as not only the "*Titanotherium* beds" (Chadronian), but also the "*Oreodon* beds" (Orellan), and possibly even "*Protoceras*

beds" (Whitneyan) deposits. In 1933, Russell and Wickenden described a Uintan-aged fauna from the nearby Swift Current River, and identified the Lac Pelletier region as possibly preserving the sediments intermediate in age between the beds of the Swift Current River and the Cypress Hills proper. Subsequently Storer described a Duchesnean fauna from this area (Storer, 1983, 1987, 1988, 1990, 1992, 1993a, 1996).

By 1950, Russell explicitly discounted the possible presence of material later than the Chadronian in the Cypress Hills Formation, based on the alleged presence of brontotheres throughout the section and the scarcity of oreodonts. It was not until the 1970s that a shift towards the publication of faunas from individual localities (Holman 1972, Storer 1978) facilitated the identification of anomalous elements in the fauna. The first unequivocally post-Chadronian fossils were some middle-Miocene ungulates described by Storer (1975a, b). Localities of Orellan, Whitneyan, Arikareean, and Hemingfordian age have since been firmly documented (Storer, 1993b, 1996), and the modern interpretation is one of relatively continuous deposition from the middle Eocene to middle Miocene.

The presence of sediment of various ages makes the need for precise locality information and sampling critical, but it is also clear that the Chadronian Age is by far the best represented in the known faunas of the Cypress Hills. Of 17 Eocene and Oligocene local faunas identified by Storer (1996), eight are Chadronian, while other ages are represented by no more than two faunas each.

Chapter 3

The Current Project

i. Sites Under Study—the Calf Creek Locality

The Calf Creek Locality is located on the north branch of Calf Creek, a tributary of Conglomerate Creek, roughly 16 km northwest of the town of Eastend (see Fig. 2.3). The legal coordinates are: legal subdivision 4, section 7, township 8, range 22 west of the 3rd meridian (longitude).

The site consists of two components. The Hunter Quarry (RSM locality 72F10-0002, ROM locality V-39), on the east side of the valley, produced the larger specimens. A screening site on the west side of the valley (RSM locality 72F10-0001, Canadian Museum of Nature locality 117, ROM V-38) produced the smaller elements of the fauna.

A formal stratigraphic column for the Calf Creek site has never been published. Williams and Dyer (1930, p. 70) briefly list measurements for the section along "Calf Creek," stating that "It is here that most of the mammal and other vertebrate remains have been found." However, this section, which is very thick, correlates only very generally with the sections known to be from the fossil localities themselves, and was presumably measured elsewhere in the creek valley. Russell (1940) lists the stratigraphic section within the quarry itself, and the section through both localities was measured around 1960 by Bruce McCorquodale (Fig. 3.1). The height above sea level given by McCorquodale for the location of the Hunter Quarry (3630-3640 feet or 1109 m above sea level) differs slightly from that given in Russell (1940) (3690 feet or 1125 m above sea level). Leckie and Cheel (1989) examined the site but found the outcrop to be degraded and buried, so did not include it in their study.

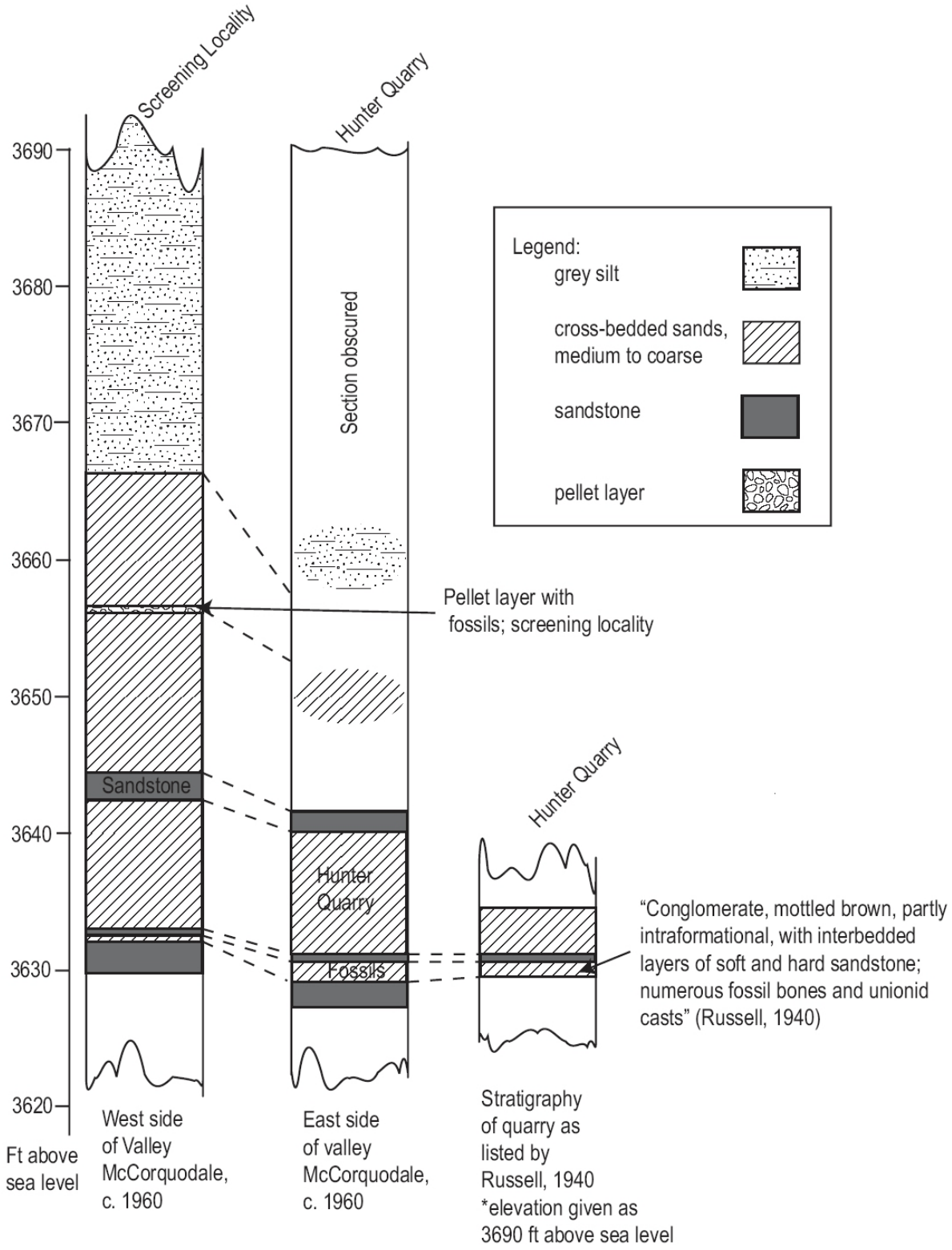


Figure 3.1—Sedimentary sections of Calf Creek, based on measurements of B. A. McCorquodale, c. 1960, and comparison with the stratigraphy as described by Russell, 1940.

The screening locality is located at a slightly higher stratigraphic level, but nothing in the extensive faunas recovered from both sites has suggested that they are not contemporaneous in age.

Although the name of the Calf Creek Local Fauna does not appear in print in until Holman (1972), the Hunter Quarry was discovered in 1936 by amateur palaeontologists Fenley and Hazel Hunter (Russell, 1940). The working of the Hunter Quarry represents the first systematic excavation of a fossil bed in the Cypress Hills, as opposed to the simple surface collecting of earlier expeditions (Russell, 1972). After its discovery the Hunter Quarry was excavated by various institutions, in particular the Royal Ontario Museum (1939, 1948,1949, 1967, 1968), the National Museum of Canada (1951, 1952) and the Saskatchewan Museum of Natural History (now RSM) (1950, 1951, 1953). At the screening locality, RSM made major collections in 1960-64 and 1966, with limited collecting since, and ROM made some collections in 1967-68 (Russell, 1972; RSM records).

The Calf Creek fauna forms the core of the "Cypress Hills Oligocene" as described by Russell (1938, 1940, 1972, 1975, 1978, 1980a, 1982, 1984), although Russell frequently included specimens from elsewhere in the formation. Storer (1993c, 1996) discusses the ramification of these inclusions, which led to misidentification of some taxa (eg. *Prosciurus relictus* as *P. vetustus, Herpetotherium fugax* as *H. valens*) and misleading age-ranges for others (eg. *Eumys*). Other publications discussing Calf Creek materials are Holman (1963, 1968, 1972), Weigel (1963), Storer (1978, 1981a & b), Emry and Storer (1981), Krishtalka et al. (1982) Storer and Bryant (1993), and Bryant (1991, 1993).

The Calf Creek Local Fauna is the most extensively studied and published from the Cypress Hills. Overall collections at the RSM consist of more than 3500 specimens. The

described fauna encompasses over 70 mammalian taxa including members of the Multituberculata, marsupials from the order Didelphimorphia, and placental orders Leptictida, Apatotheria, Insectivora (Lipotyphla), Palaeanodonta, Creodonta, Carnivora, Perissodactyla, Artiodactyla, Rodentia, and Lagomorpha (Storer, 1996). Weigel (1963) described a quail, a sandpiper, and a cuckoo from the site, and Holman (1972) identified 17 species of amphibians and reptiles, including salamanders, frogs, turtles, crocodiles, lizards, and snakes.

Table 3.1— "Insectivore" taxa from the Calf Creek Local Fauna. Identifications from Storer (1996).

Order Leptictida
- Family Leptictidae
  - *Leptictis* cf *L. acutidens* (Douglass 1901)

Order Apatotheria
- Family Apatomyidae
  - ?*Apatemys* sp.
  - *Sinclairella* sp.

Grandorder Lipotyphla
- Order Erinaceomorpha
  - Family Sespedectidae
    - Subfamily Scenopaginae
      - *Ankylodon* sp.
- Order Soricomorpha
  - Family Geolabididae
    - *Centetodon* cf. *C. magnus* Marsh 1872
  - Superfamily Soricoidea
    - Family Micropternodontidae
      - *Micropternodus* sp.
    - Family Apternodontidae
      - *Oligoryctes* sp.
      - *Apternodus* sp.
    - Family Soricidae
      - Subfamily Heterosoricinae
        - *Domnina* sp.
    - Family incertae sedis
      - *Cryptoryctes* sp.

Order Chiroptera
- Family Molossidae
  - *Wallia* sp.

The current project has expanded on the descriptions (Russell, 1972) and identifications (Storer, 1996, see Table 3.1) of members of the Leptictida, Apatotheria, Lipotyphla, and also Chiroptera. The material consists of over 130 specimens falling into as many as 13 taxa.

According to Storer (1996), the Calf Creek is of younger age than the Southfork (Cypress Hills), Yoder (Wyoming), Titus Canyon (California), and McCarty's Mountain (Montana) local faunas and the Dry Hole Quarry at Flagstaff Rim (Wyoming) (all late early Chadronian of Prothero and Emry (2004)), based on the occurrence at Calf Creek of *Leptomeryx*

speciosus and *L. mammifer* rather than *L. yoderi*. It is older than the Pipestone Springs fauna (Montana, middle Chadronian of Prothero and Emry (2004)), based on several species present, including the rodent *Ischyromys junctus.* Storer (1996) argued for the placement of the locality within the latest early Chadronian on the basis of several taxa, including *Yoderimys stewarti* (limited to late early Chadronian of Prothero and Emry (2004)), but chose to follow earlier workers in assigning it to the middle Chadronian. Given the presence of *L. mammifer, Prosciurus vetustus, Hyaenodon microdon* (all limited to the middle Chadronian according to Prothero and Emry (2004)) and *Paleolagus temnodon, Miohippus grandis,* and *Megalagus* cf. *M. Brachyodon*, which first occur in the middle Chadronian, according to Prothero and Emry (2004), this age seems most likely. The new identifications of species accord well with this interpretation. The precise implications are discussed in Chapter 6.

ii. Sites Under Study—the Horse Locality

Table 3.2—Insectivore taxa from the Horse Local Fauna. Identifications from Storer (1996).

Leptictida
  Leptictidae
    Leptictis sp.

The Horse Locality is named for a partially-articulated *Mesohippus* skeleton recovered by the Tyrrell Museum in 1983. It is found roughly 15 km north and slightly east of the Calf Creek at legal subdivision 1, section 7, township 9, range 22 west of the 3rd meridian. The locality consists of a number of roadside exposures along a mile of grid road (Fig. 2.3 and 3.2). The area is generally flat, but a slight slope across the area and minor excavations allowed Frank McDougall to measure roughly 16 m of geological section and demonstrate a general correlation between the fossiliferous layers (McDougall, 1995) (Fig 3.3). The bulk of the collection comes from the

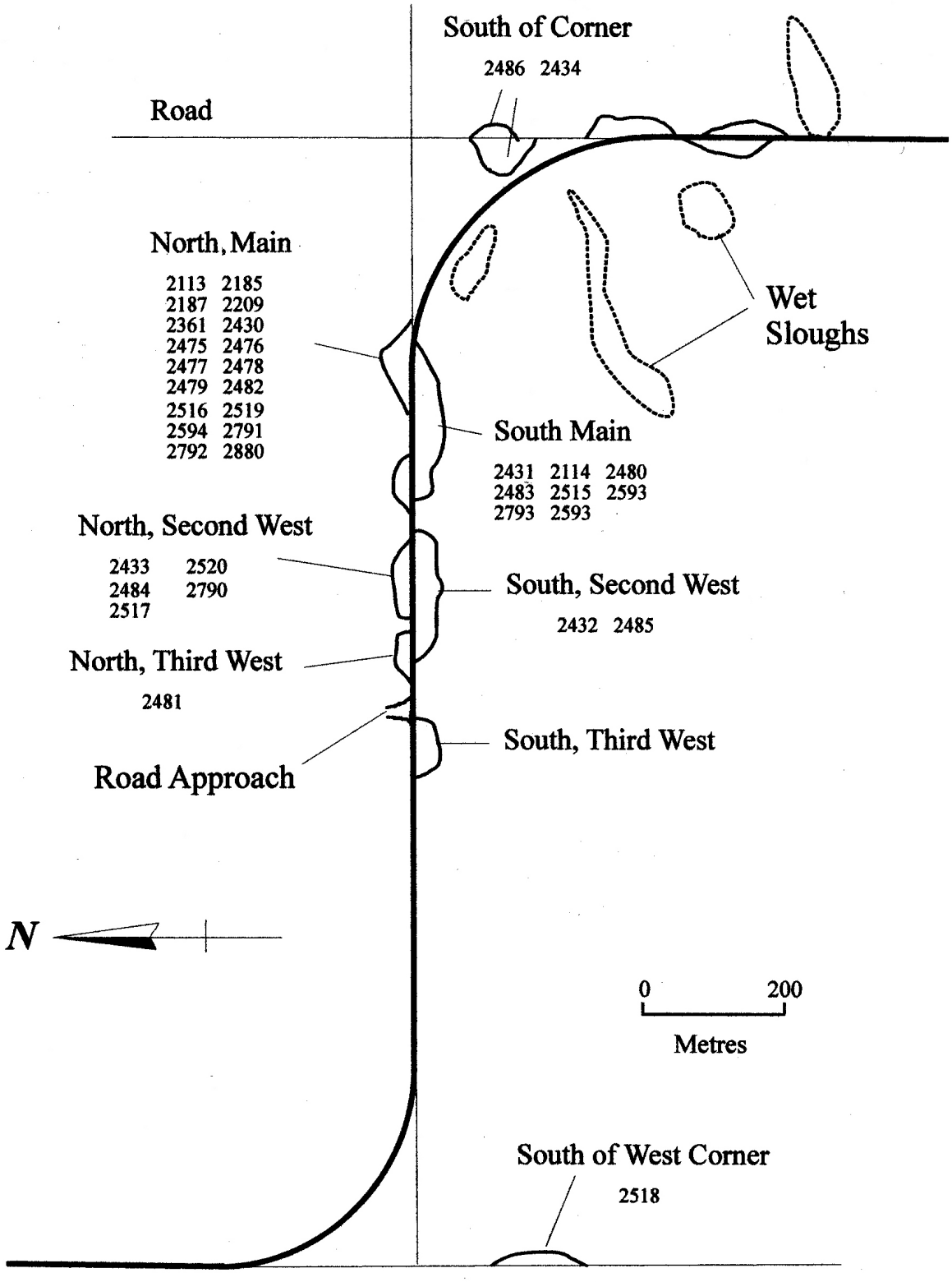


Figure 3.2— Map of the Horse Locality, with RSM P-numbers. Map prepared by Frank McDougall, 2005.

North Main pocket, but separate locality and collection data was recorded for each of the individual pockets. RSM locality numbers for the site are as follows: 72F15-0004, North Main pocket (the Horse Locality in the restricted sense and the source of most of the fossils); 72F15-0005, South Main (the source of the *Mesohippus* collected by the Tyrrell); 72F15-0007, North, Second West and North, Third West; 72F15-0003, South, Second West; 72F15-0008, South of Corner.

The only published reference to the Horse Locality (Storer, 1996) includes it with the nearby Carnagh local fauna (RSM locality no. 72F15-0002), based on preliminary faunal similarities and close proximity; the Carnagh Locality is located about 1.5 miles (2.4 km) north along the highway, in what is probably the same stratigraphic layer (see Fig. 2.3). However, the Carnagh Locality consists of a single small roadcut exposure that has produced only a very limited minor assemblage (20 specimens in RSM collections), while the several pockets of the Horse Locality have produced a diverse fauna in the range of 2500 specimens. Given the negligible importance of the Carnagh Locality and the desirability of highly specific locality information, the name "Horse Local Fauna" is retained here as a separate unit.

Like the fossils from the Calf Creek screening locality, most of the specimens from the Horse Locality are disarticulated and fragmented bones and isolated teeth, although some articulated material, including the *Mesohippus* skeleton, came from the South Main pocket. Approximately 120 specimens are referred to the groups of interest to this study.

After the initial discovery of the site by the Tyrrell Museum in 1983, further exploration was undertaken by John Storer and Tim Tokaryk of RSM in the summer of 1988 (RSM collection P2113). Frank McDougall continued collecting at the site between 1992 and 1995 as

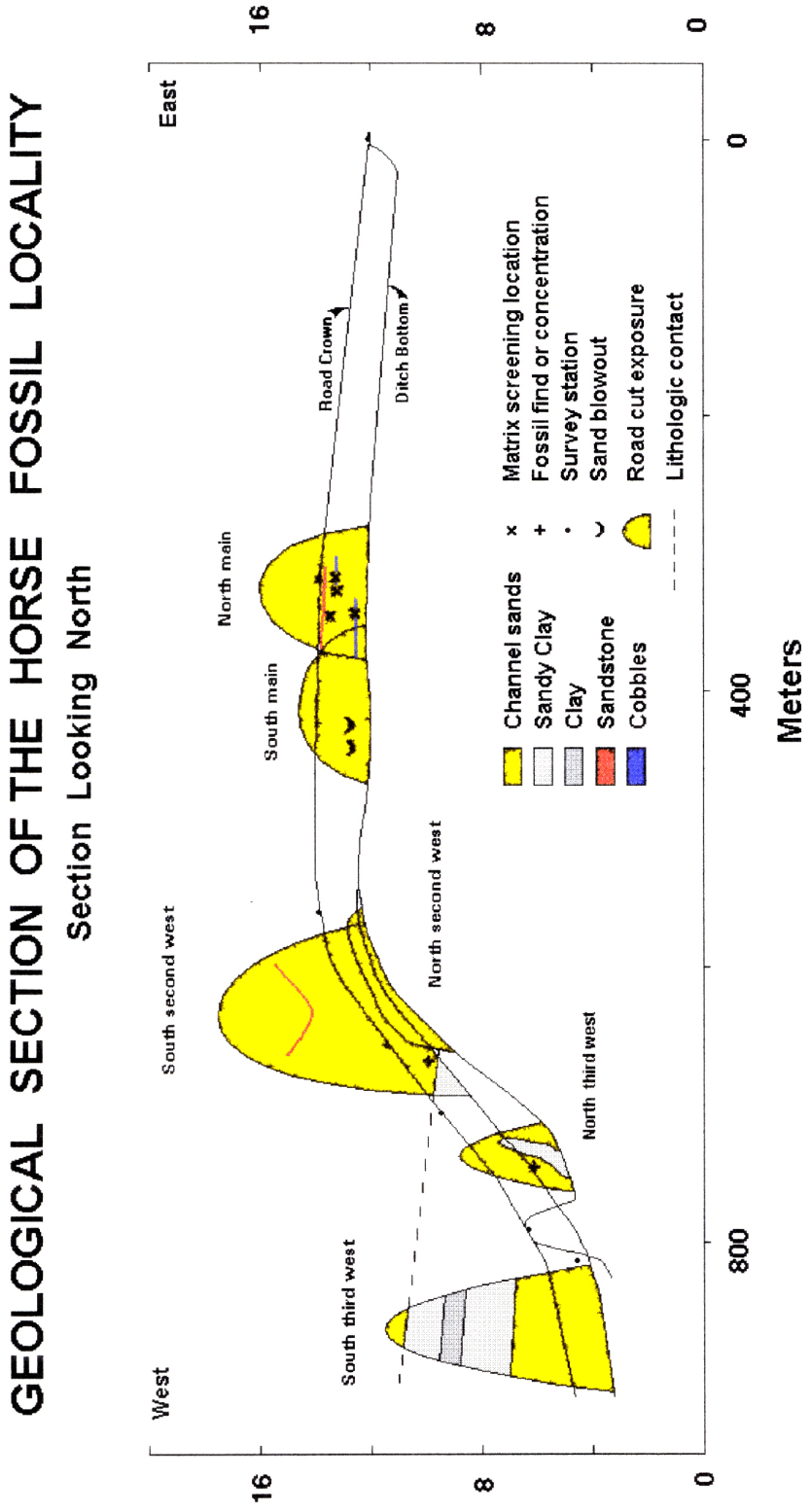


Figure 3.3—Stratigraphic section of the Horse Locality, from McDougall (1995). Both scales in m.

part of ongoing PhD work. The other P numbers illustrated in Fig. 3.2 represent McDougall's work.

Although only the most preliminary identifications had been made at that time, Storer (1996) listed the following orders as present at the Horse Locality: Multituberculata, Didelphimorphia, Leptictida, Carnivora, Perissodactyla, Artiodactyla, Rodentia, and Lagomorpha. Of the "insectivore" groups, only Leptictida was known. The current study of the "insectivore" sample from the Horse Locality has identified a fauna of similar abundance and diversity to that of the Calf Creek. The Horse Local Fauna is considered slightly younger than the Calf Creek based on the identification of *Ischyromys veterior,* a rodent species slightly more advanced than the *Ischyromys junctus* identified from Calf Creek (Storer 1996). Storer (1996) placed the site later within the middle Chadronian. Frank McDougall (pers. comm. 2005) considers the site to be late Chadronian, based on the presence of *Mesohippus* cf. *M. bairdi* and characteristics of the brontotheres. However, the presence of *Leptomeryx mammifer* and *Prosciurus vestustus*, both of which are considered limited to the middle Chadronian by Prothero and Emry (2004), appear to place the Horse Local Fauna within that period. *Mesohippus bairdi* is listed as first occurring in the late Chadronian (Prothero and Emry, 2004).The transitional nature of *Mesohippus* cf. *M. bairdi* at the Horse Locality may indicate an age at the very end of the middle Chadronian. The current "insectivore" identifications are compatible with a middle Chadronian fauna, possibly somewhat later within the middle Chadronian.

iii. Justification for Comparison

The Calf Creek and the Horse localities are the two best-sampled sites of Chadronian age in the Cypress Hills region. In particular, both sites possess extensive collections of small

mammals, and are the only two sites of their age with enough “insectivore” specimens to permit a reasonably complete description and comparison of that component of the faunas.

Since both sites most likely occur within the middle Chadronian and are in the same geographic area, the detection of any faunal change between them would add resolution to the picture of faunal succession within the Chadronian, while largely eliminating the variable of geographic differences in faunal composition.

iv. Goals of this Project

This project aims to:

- formally identify and describe the "insectivores" (Apatotheria, Leptictida, Lipotyphla) and Chiroptera of the Calf Creek and Horse Local Faunas.
- assess faunal change between the two sites, if any.
- assess the implications of any faunal change in the “insectivores” with regards to the ages of the two sites.
- describe the “insectivore” fauna for the middle Chadronian in the Cypress Hills to a) facilitate greater use of “insectivores” in correlation of North American fossil sites of this age, and b) add to the resolution of the record of species change within the middle Chadronian if differences between the two faunas are confirmed.

v. Materials and Methods

Materials:

The primary materials consist of the existing collections of “insectivore” specimens from both localities. These are mostly isolated teeth, a few jaws, and limb elements, roughly 130

specimens from the Calf Creek Locality and 120 specimens from the Horse Locality. Major collections are from RSM; Calf Creek Locality specimens in the collections at ROM were also borrowed for identification.

Comparative material was borrowed from other museums: the Royal Ontario Museum, the National Museum of Natural History, the Carnegie Museum, the Field Museum, the Texas Memorial Museum, and the American Museum of Natural History; a personal visit by the author to the collections of the American Museum of Natural History was also invaluable.

Methods:

The "insectivore" specimens from the Calf Creek Locality had already been identified as far as genus with a fair degree of certainty. Most insectivore specimens from the Horse had also been recognized, although not identified, but re-examination of unmounted material, including isolated teeth and small limb bones, was undertaken to identify any overlooked elements, particularly upper molars belonging to *Oligoryctes* and humeri of *Cryptoryctes;* both these items were found during this re-examination. A brief re-examination of limb-girdle elements from both localities was also attempted, in the hopes of recovering other elements of the forelimb of *Cryptoryctes* using the methodology described in Reed (1965); this attempt was not successful.

Specific identification has been based on direct comparison with type/paratype material wherever possible and with reference to the literature. Visual characteristics, measurements, and descriptions have been taken into account. Variation in the taxa between the two sites has been noted.

Measurements were taken with a micrometer disc inserted into the eyepiece of a Leitz dissecting microscope. Most measurements were taken at 40X, at which magnification the

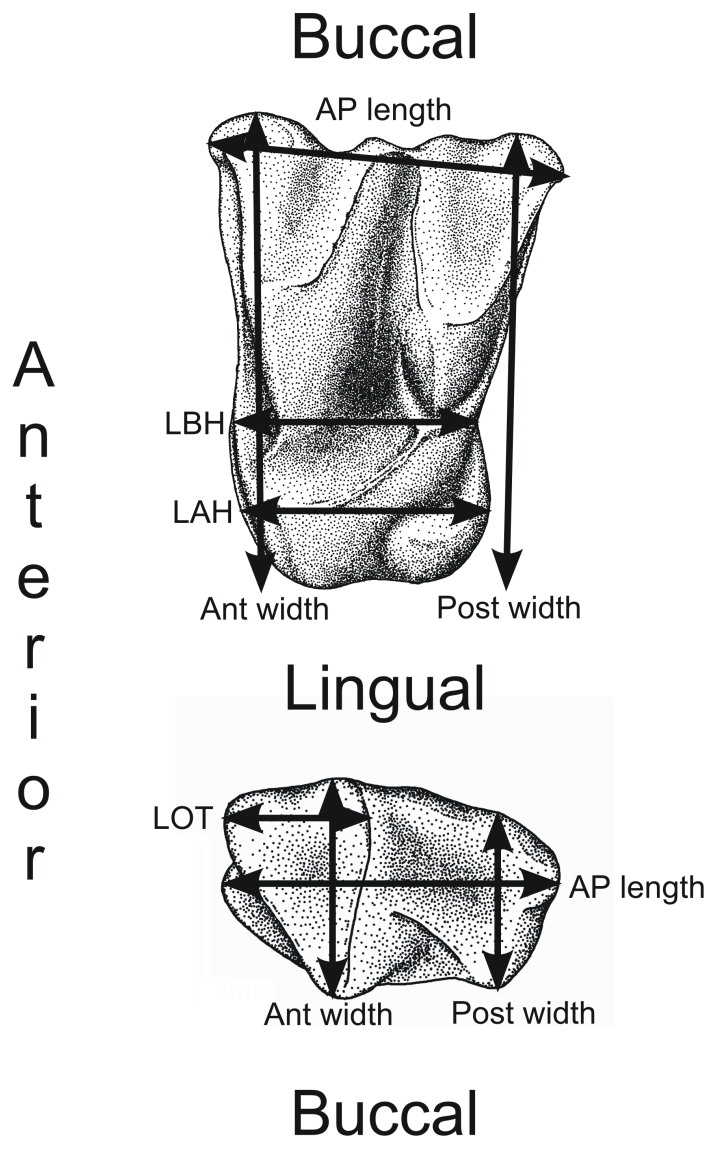


Figure 3.4—Orientations of measurements for upper and lower molars. AP length: anteroposterior length; Ant width: anterior width; Post width: posterior width; LBH: length buccal to hypocone; LAH: length at hypocone; LOT: length of talonid.

micrometer increments correspond to .026 mm. Thus while measurements are reported to .01 of a mm, actual accuracy is ±0.03. Due to field of view issues, larger teeth, particularly those belonging to *Leptictis* and *Sinclairella*, could only be measured under the 10X magnification; these measurements are accurate to .1 mm. See Fig. 3.4 for orientations of measurements; which measurements were taken varies depending on tooth morphology.

Tooth positions are referred to using the terminology of Jepsen; upper teeth are indicated by upper case letters (P for premolars, M for molars) and lower teeth by lower case letters (p and m).

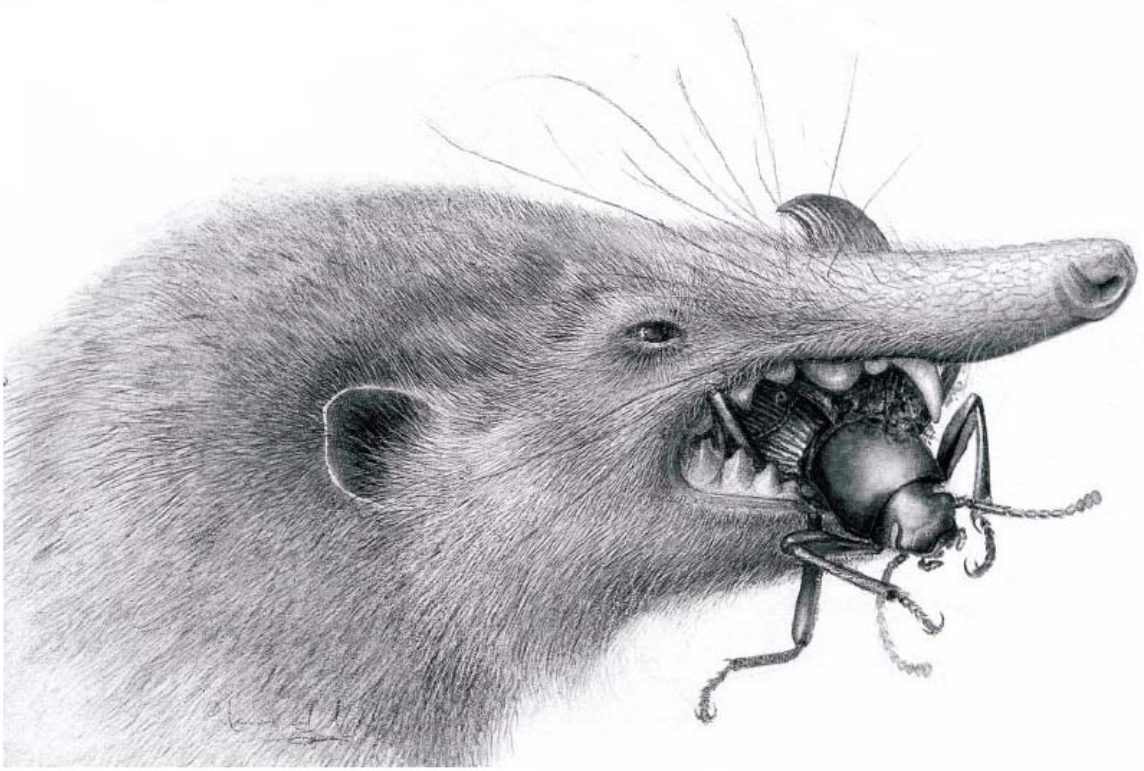


Figure 4.1---*Apternodus baladontus*, reconstruction by Chester Tarka, from Asher et al. (2002).

Chapter 4.

What is an insectivore?

Reference has already been made to the term "insectivore." However, no concise definition of that term has been given—partly because it is a particularly troublesome term biologically and historically. For the purposes of the current research it has a purely functional definition; it refers to a diverse group of small mammals which have been identified from the Calf Creek Local Fauna but never thoroughly described; and their comparable taxa from the Horse Local Fauna. In a broader sense it is a term for an alleged order of mammals, the Insectivora, a motley and unstable grouping mostly united by primitive characteristics, generally

considered to include the modern shrews (Soricidae), moles (Talpidae), hedgehogs (Erinaceidae), solenodons (Solenodontidae), sometimes the African tenrecs (Tenrecidae) and golden moles (Chrysochloridae), and a variety of fossil generalized placental mammals showing no particular affinity to any other order (Figure 4.1). A discussion of the tortuous taxonomic history of this group is given under the heading "Insectivore Phylogeny," but first a brief overview of the generalized morphology and possible synapomorphies of the "insectivores" will be provided.

In contrast to the Insectivora, the Chiroptera are an easily-recognized, well-defined mammalian group. The identifications and descriptions in this thesis include several chiropteran taxa due to their dental similarity to insectivores and their presence within the group of undescribed Calf Creek specimens, but the particulars of chiropteran phylogenetic and taxonomic history are not addressed below.

i. Insectivore Morphology

It has long been recognized (eg. Butler, 1972) that the Insectivora represented a wastebasket taxon to which most generalized early placental mammals of dubious affinity were assigned. Thus most animals which have at one time or another been considered insectivores have what is often described as a "generalized placental body plan." They have tribosphenic molars with dilamdodont (Fig. 4.2) or zalamdodont uppers (Fig. 4.3), relatively small brains, retain five-digit, clawed feet, and most are small to very small—no bigger than a cat, and including some of the smallest mammals in the world. Some efforts have been made to identify possible synapomorphies of modern insectivores, including a reduced pubic symphysis, reduced digestive system lacking a caecum, and a flexible proboscis; however, none of

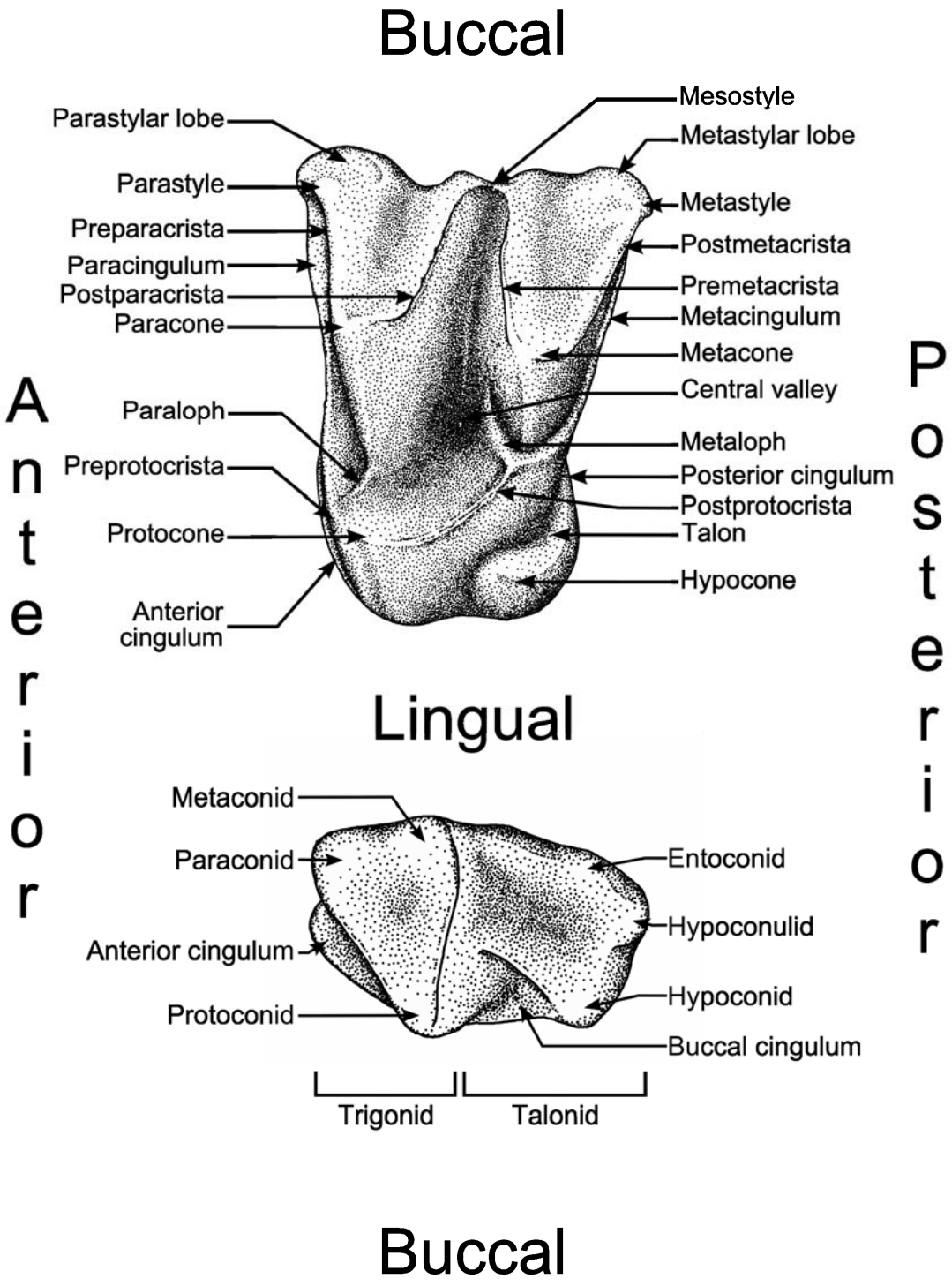


Figure 4.2—Tribosphenic molars with morphology labelled. Dilamdodont left upper molar (top); left lower molar (bottom).

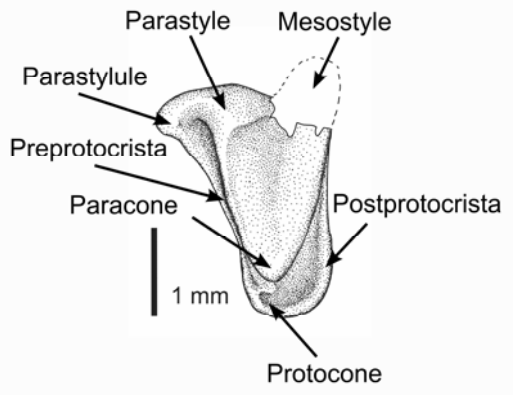


Figure 4.3—zalamdodont left upper molar; same orientation as Fig. 4.2 top.

these characteristics are particularly useful in identifying fossils, since two are soft-tissue and well-preserved pelvic material is rather rare in fossil micromammals.

ii. Insectivore Phylogeny

Probably no other group of mammals has a taxonomic history as convoluted and unstable as the diverse taxa which have, at one time or another, been united under the umbrella of the "Insectivora." Throughout the nearly two hundred years since the order was first recognized, the number of taxa considered to be insectivores, which groups, and in what arrangement, has varied immensely (Table 4.1). The most obvious reason for this variation is the lack of obvious attributes in common. Most traditional insectivore groups are united by little more than generally small size, animalivore diet, and a general impression of "primitiveness." This generalized state made it possible to view the Insectivora as the basal ancestral stock of the eutherian tree, where any generalized placental that did not clearly belong to another order could be placed, and led to the use of the Insectivora as a wastebasket for generalized eutherian mammals.

Linnaeus grouped moles, shrews, and hedgehogs together by 1758, but under various names and with various other taxa (McKenna and Bell, 1997). Illiger, in 1811, added tenrecs and golden moles, under the name "Subterannea" (Gregory, 1910). "Les Insectivores" was coined by de Blainville in 1816 (Gregory, 1910), and the most common term, Insectivora, appeared in Bowdich in 1821 (Butler, 1972). This basic grouping (moles, shrews, hedgehogs, tenrecs, and

golden moles) can be considered the core of the Insectivora. However, other small, generalized groups such as the tree shrews (Tupaiidae), elephant shrews (Macroscelididae), and even colugos (Dermoptera) were gradually included. These new additions had some different features, however, and by 1866 Haeckel divided the Insectivora into the Lipotyphla, the original insectivores, which lack a caecum, and the Menotyphla, the tree shrews and elephant shrews, which have a caecum. In the late 1800s the solenodons (Solenodontidae) of the Caribbean were also recognized as a separate group of Lipotyphlan insectivores (Gill, 1872 and Dobson, 1882; both in Gregory, 1910). Gill also divided the Lipotyphlans into the Zalambdodonta and Dilamdodonta, based on tooth structure (Fig. 4.2, 4.3) (Gill, 1872, in Gregory 1910).

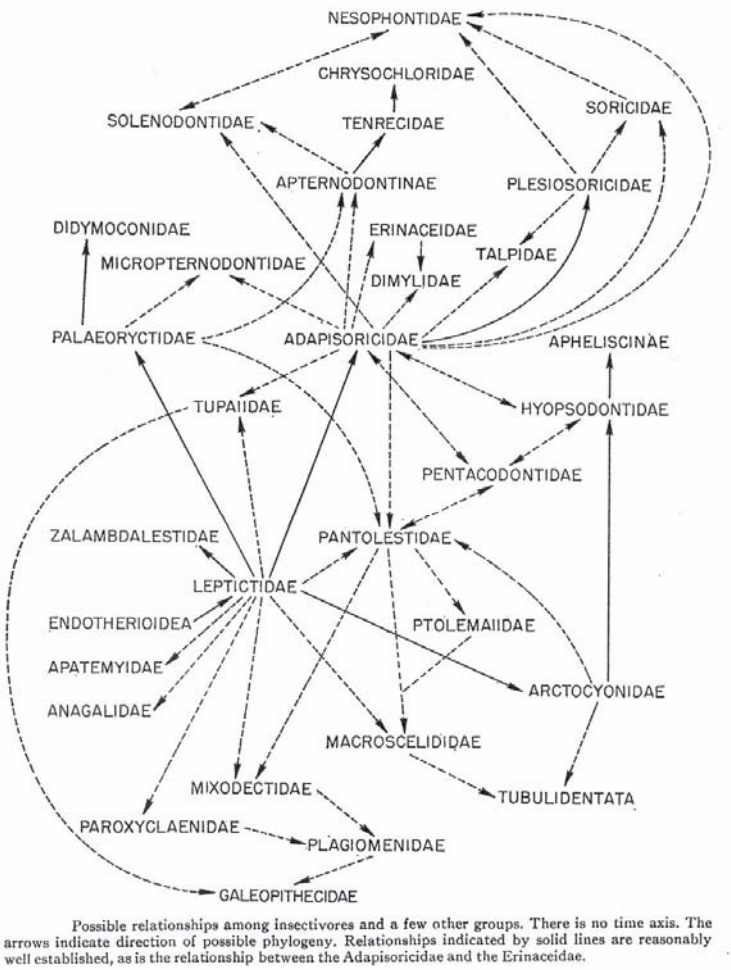
Huxley (1880) discussed the resemblance of early members of other lineages to insectivores and the problems of identifying the ordinal position of very early mammals. He stated that many early mammals fit neatly into no recognized orders, but came closer to the Insectivora than to any others, describing the insectivores as “central” to the Eutheria, and stating that they “departed but little from the general type.” (Huxley, 1880, p. 65).

However, Huxley also felt that each lineage passed separately through a series of grades from pre-mammalian forebears on, with some modern forms being of more advanced grade than others. This view does not seem to allow for different orders branching from a common ancestor, so the Insectivora were not seen as ancestral so much as less advanced, possessing a modern form most similar to that seen in the past of other groups.

By the time of Gregory (1910), however, this “centrality” had become explicitly modified into an ancestral condition, and the Insectivora was seen as the group from which all other eutherian mammals were most likely descended. This concept led to the use of the taxon as a

Table 4.1—Early classifications of insectivores, as reproduced in Gregory, 1910. Taxa relevant to the current thesis are in bold

Illiger, 1811	**Haeckel, 1866**	**Gregory, 1910**
Ordo XI—Volantia Fam. Dermpoptera (*Galeopithecus*) Fam. Chiroptera (*Pteropus, Harpyia, Vespertilio, Nycteris, Rhinolophus,Phyllostomus, Noctilio, Saccopteryx, Dysopes*) Ordo XII—Faculata **Fam. Subterannea** (*Erinaceus,Centetes, Sorex, Myogale, Condylura, Chrysoschloris, Scalops, Talpa*.) Fam. Plantigrada (*Cercoleptes, Nasua, Procyon, Gulo, Meles, Ursus*) Fam. Sanguinaria (*Megalotis, Canis, Hyaena, Felis, Viverra, Ryzaena*) Fam. Gracilia (*Herpestes, Mephitis, Mustela, Lutra*)	**Class Mammalia** I. Subclass: Ornithodelphia s. Amasta (Monotremata) II. Subclass: Didelphia s. Marsupialia **III. Subclass: Monodelphia s. Placentalia** 1.Legio: Indecidea (Edentata, Fyenoderma) 2.Legio: Deciduata Zonoplacentalia I. Ordo: Chelophora II. Ordo: Carnaria **Discoplacentalia** I. Ordo: Prosimiae (inc. *Galeopithecus*, aka Dermoptera) II. Ordo: Rodentia **III. Ordo: Insectivora** I. Subordo: Menotyphla, H. 1. Familia: Cladobatida s. Scandentia (Cladobates, Tupaia) 2. Familia: Macroscelidea s. Salientia (*Macroscelides, Rhynchocyon*) **II. Subordo: Lipotyphla**, H. 1. Familia: Soricida (*Sorex, Crossopus, Crocidura*) 2. Familia: Talpida (*Talpa, Condylura, Chrysochloris*) 3. Familia: Erinaceidea (*Erinaceus, Gymnura*) 4. Familia: Centetida (*Centetes, Solenodon*) IV. Ordo: Chiroptera (Volantilia) V. Ordo: Simiae	**Class Mammalia** Linn. Subclass Promammalia Subclass Prototheria Gill, Huxley **Subclass Theria** Parker & Haswell (= Eutheria Gill) I. Infraclass Metatheria Huxley **II. Infraclass Eutheria** Huxley (Monodelphia Blainv., Placentalia auct.). **Superorder Therictoidea** **Order Insectivora** (Gray). **Suborder Lipotyphla** Haeckel. **Section -----.** Fam. Pantolestidae **Section Zalamdodonta** Gill. Fam. Centetidae Fam. Potamogalidae Fam. Solenodontidae Fam. Necrolestidae Fam. Chrysochloridae **Section Erinaceomorpha** Fam. Leptictidae Fam. Erinaceidae Fam. Dimylidae **Section Soricomorpha** Fam. Soricidae Fam. Talpidae **Section ----------.** Fam. Hyopsodontidae. Order Ferae Linn. (1758) Carnivora auct. Suborder Creodonta Cope. Suborder Fissipedia (Blumenbach). Carnassi dentia Wortman (In part) Suborder Pinnipedia (Storr) Illiger. Superorder Archonta Order Menotyphla Haeckel Family Tupaiidae Family Macroscelididae Incertae sedis. Family Mixodectidae Order Dermoptera Illiger Family Galeopithecidae Order Chiroptera Order Primates



Possible relationships among insectivores and a few other groups. There is no time axis. The arrows indicate direction of possible phylogeny. Relationships indicated by solid lines are reasonably well established, as is the relationship between the Adapisoricidae and the Erinaceidae.

Figure 4.4—Possible relationships among insectivores, from Van Valen (1967). Original caption reads: "Possible relationships among insectivores and a few other groups. There is no time axis. The arrows indicate direction of possible phylogeny. Relationships indicated by solid lines are reasonably well established, as is the relationship between the Adapisoricidae and the Erinaceidae."

"wastebasket" for poorly-known or otherwise enigmatic specimens (Simpson, 1945; Butler, 1972), and many fossils of unclear affiliation, such as the leptictids and apatemyids, were assigned, however tentatively, to the Insectivora. At the same time it was acknowledged that relationships within the Insectivora were equally poorly understood (Van Valen, 1967) (Fig. 4.4).

In the last thirty years, the shift towards the cladistic method and a growing emphasis on the importance of natural, monophyletic groupings as the basis of classification have led to a movement away from the use of wastebasket taxa in general, and within the Insectivora specifically (Butler, 1972; McKenna, 1975). The menotyphlans, as well as the more troublesome fossil groups, were pared off, sectioned into their own orders (Macroscelidea, Scandentia, and Dermoptera, and the fossil Leptictida and Apatotheria) or left

Table 4.2—Insectivore classifications of Van Valen (1967, shown to family level) and McKenna and Bell (1997, shown to order).

Van Valen (1967)	McKenna and Bell (1997)
Order Insectivora (G. Cuvier, 1817) Illiger, 1811 **Suborder Proteutheria** (Romer, 1966) Superfamily Endotherioidea (Shikama, 1947) Family Endotheriidae Family Pappotheriidae **Superfamily Tupaioidea** (Gray, 1825) **Leptictidae** Zalambdalestidae Anagalidae Paroyclaenidae Tupaiidae Pantolestidae Ptolemaiidae Pentacodontidae Superfamily Apatemyoidea **Apatemyidae** Suborder Macroscelidea Butler, 1956 Macroscelididae Suborder Dermoptera Illiger, 1811 Superfamily Mixodectoidea Mixodectidae Superfamily Galeopithecoidea Plagiomenidae Galeopithecidae **Suborder Erinaceota** Van Valen, 1967 **Superfamily Erinaceoidea** Fischer von Waldheim, 1817 Adapisoricidae Erinaceidae Dimylidae Talpidae **Superfamily Soricoidea** Fischer von Waldheim, 1817 Plesiosoricidae Nesophontidae **Soricidae** **Order Deltatheridia** Suborder Hyaenodonta Superfamily Palaeoryctoida Palaeoryctidae **Micropternodontidae** Didymoconidae Superfamily Hyaenodontoidea Hyaenotontidae Superfamily Oxyaenoidea Oxyaenidae **Suborder Zalamdodonta** Superfamily Tenrecoidea Tenrecidae Solenodontidae Superfamily Chrysochloroidea Chrysochloridae	**Magnorder Ernotheria** McKenna, 1975 Superorder Kennalestida McKenna, 1975 **Superorder Leptictida** McKenna, 1975 **Grandorder Ictopsia** McKenna, 1975 Grandorder Anagalida Szalay and McKenna, 1971 Order Macroscelidea Order Lagomorpha **Magnorder Preptotheria** McKenna, 1975 Superorder Deltatheridia Van Valen, 1965 **Superorder Tokotheria** McKenna, 1975 **Grandorder Ferae** Linnaeus, 1758 **Order Cimolesta** McKenna, 1975 Suborder Didelphodonta McKenna, 1975 Suborder Pantodonta Cope, 1873 Suborder Pantolesta McKenna, 1975 **Suborder Apatotheria** McKenna, 1975 Suborder Taeniodonta Cope, 1876 Order Creodonta Cope, 1875 Order Carnivoria Bowdich, 1821 **Grandorder Insectivora** Illiger, 1811 **Order Erinaceomorpha** Gregory, 1910 **Order Soricomorpha** Gregory, 1910 Grandorder Archonta Gregory, 1910 Order Scandentia Wagner, 1855 Order Dermoptera Illiger, 1811 **Order Chiroptera** Blumenback, 1779

dangling "incertae sedis," until by the time of Butler (1988) an apparently monophyletic core consisting of the Soricidae, Talpidae, Erinaceidae, Solenodontidae, Chrysochloridae, and Tenrecidae, and select fossil groups, was left, the same grouping initially recognized in the early 1800s, with the exception of the solenodons and fossil members. However, to distinguish it from the inflated concept of "Insectivora," this remnant is frequently referred to as the Lipotyphla. Butler (1988) and MacPhee and Novacek (1993) attempted to define Lipotyphla as a monophyletic clade based on morphological synapomorphies for the Lipotyphla, but had limited success. Butler (1988) suggested nine possible synapomorphies; however, none were dental and many were soft-tissue, again making their assessment in fossil groups difficult or impossible. MacPhee and Novacek (1993) questioned all but two of Butler's (1988) synapomorphies, simplified gut tube and reduced pubic symphysis, but agreed with a monophyletic Lipotyphla. They also suggested that the Carnivora might be the most likely candidate for sister-group to the Lipotyphla + Leptictida.

At this point, the modern groups referred to the Lipotyphla correspond more or less exactly (allowing for the addition of the Solenodontidae as a separate family) to the order Insectivora as it was first envisioned by Illiger and de Blainville, almost two hundred years previous. During this time the affinity of these diverse families has only seldom been questioned (most notably by Van Valen (1967), who tentatively removed the Chrysochloridae, Tenrecidae, and Solenodontidae to his Deltatheridia). However, with the onset of molecular techniques of assessing phylogeny, some surprising results were suggested.

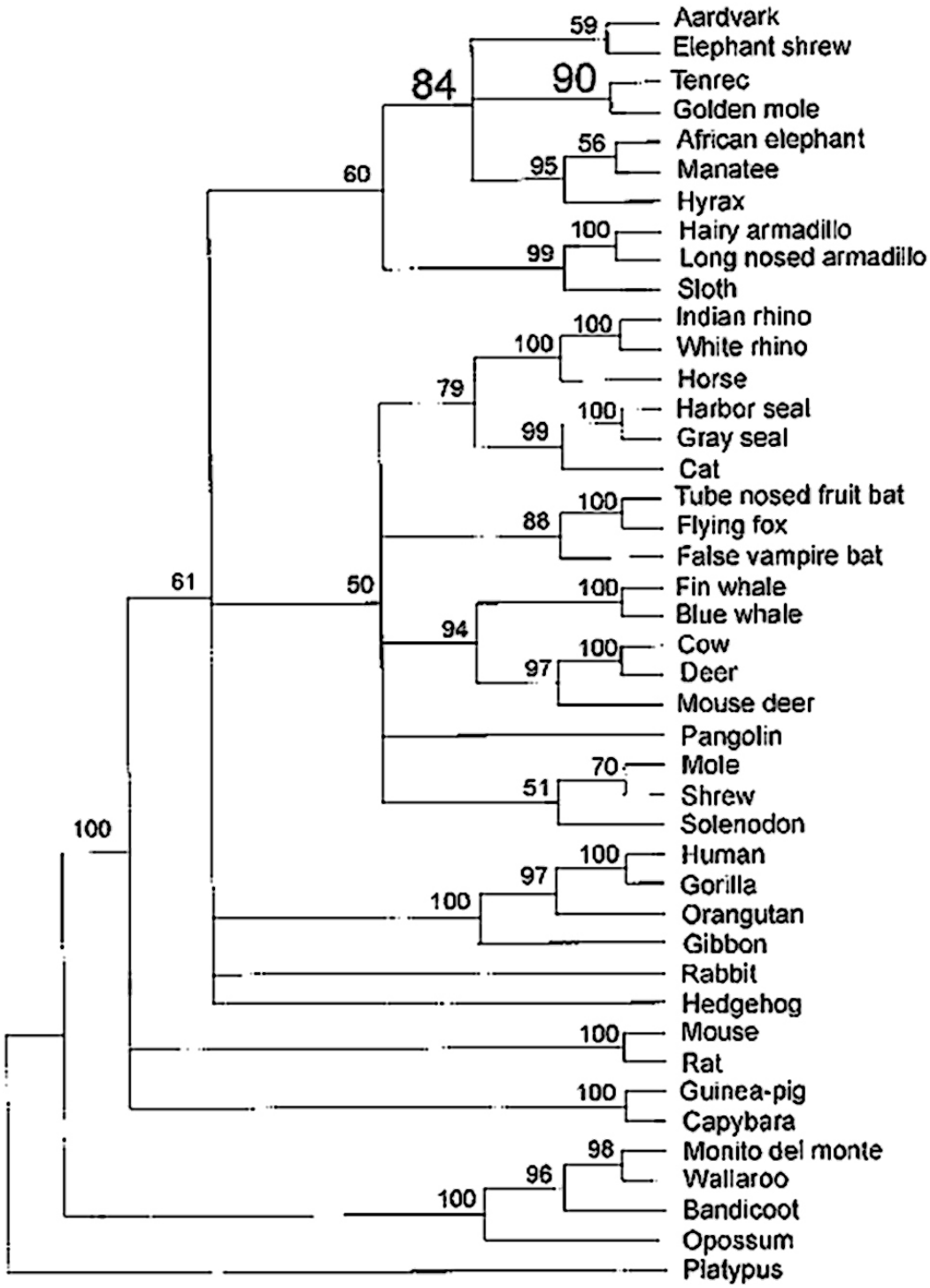


Figure 4.5—Cladogram of Stanhope et al. (1998) showing Afrotheria including Chrysochloridae and Tenrecidae, and hedgehog separate from shrew, mole, and solenodon clade.

In the late 1990s, molecular studies by Springer et al. (1997, using mitochondrial DNA) and Stanhope et al. (1998, on both nuclear and mitochondrial DNA; Fig. 4.5) aimed at addressing intra-ordinal relationships in placental mammals. Although most traditional higher-scale groupings were recovered, two surprising results emerged in both studies. The first was a group of various African mammals which had not generally been recognized to have any special relationships: elephants, sirenians, hyracoids, aardvarks, and elephant shrews. The second was that this African clade also included two African insectivore groups, the tenrecs and golden moles, and so rendered the traditional Lipotyphla polyphyletic. This African group is now generally termed the Afrotheria. Although the term Lipotyphla is still correct when restricted to the Soricidae, Talpidae, Solenodontidae, and Erinaceidae, the term "Eulipotyphla" is often applied to denote only these four groups (and demonstrable fossil relatives), as distinct from the traditional, broader usage of Lipotyphla.

Although subsequent studies have not always strongly supported the Afrotheria (or other more traditional ordinal groups) (e.g. Emmerson et al., 1999), the lack of recognition of a recognizable Lipotyphla of any kind in many studies is striking. Mouchatty et al. (2000) found the hedgehogs to be the sister-group to all other mammals, while moles were the sister-group of bats. Waddell et al. (1999) also failed to return a monophyletic Lipotyphla. Douady and Douzery (2003) examined a larger group of mammals, and recovered a separate Afrotheria including the Tenrecoidea, as well as a Eulipotyphla of moles, shrews, and hedgehogs. Their molecular clock estimates of divergence times suggested an origin for the Eulipotyphla in the mid-Cretaceous and the divergence of the moles by the late Cretaceous.

At the same time as molecular data often appeared to be tearing the Lipotyphla apart, efforts to discover morphological support for the new Afrotherian clade and a polyphyletic Lipotyphla were having little success. Whidden (2002) dissected snout musculature of extant lipotyphlans and various "afrotheres" to explore the nature of the flexible proboscis that had been suggested as a possible synapomorphy for both clades. He found support for the traditional Lipotyphla (including tenrecs and golden moles) in the structure of the muscles which controlled snout-movements in these groups, but found that the afrotheres, although they all displayed flexible noses, varied in the structure and organization of their snout musculature.

Asher et al. (2002) performed an extensive morphological analysis on living and fossil lipotyphlans. Although not designed to test the monophyly of Lipotyphla and lacking chrysochlorids, this analysis produced some interesting results. The successive outgroups of *Didelphis* followed by macroscelidids, were consistently maintained outside a core of lipotyphlans. Erinaceids were the outgroup to other Lipotyphlans, with *Micropternodus* falling either one node up or unresolved with them. Palaeoryctids appeared next, well within Lipotyphla, with *Centetodon* next. The *Nesophontes-Solenodon* clade suggested by McDowell (1958) did not appear, and ordered and unordered analyses differed as to whether Tenrecidae or Solenodontidae were the immediate sister-group to the soricids and apternodontids.

Asher et al. (2003) examined a much larger group of mammals in a combined morphological-molecular analysis, to permit the inclusion of fossil taxa. Even so, the Afrotheria were recovered relatively robustly. The Eulipotyphla generally grouped together, also. The position of *Leptictis* in this analyses is interesting: it is either unresolved or near the Macroscelidea within Afrotheria.

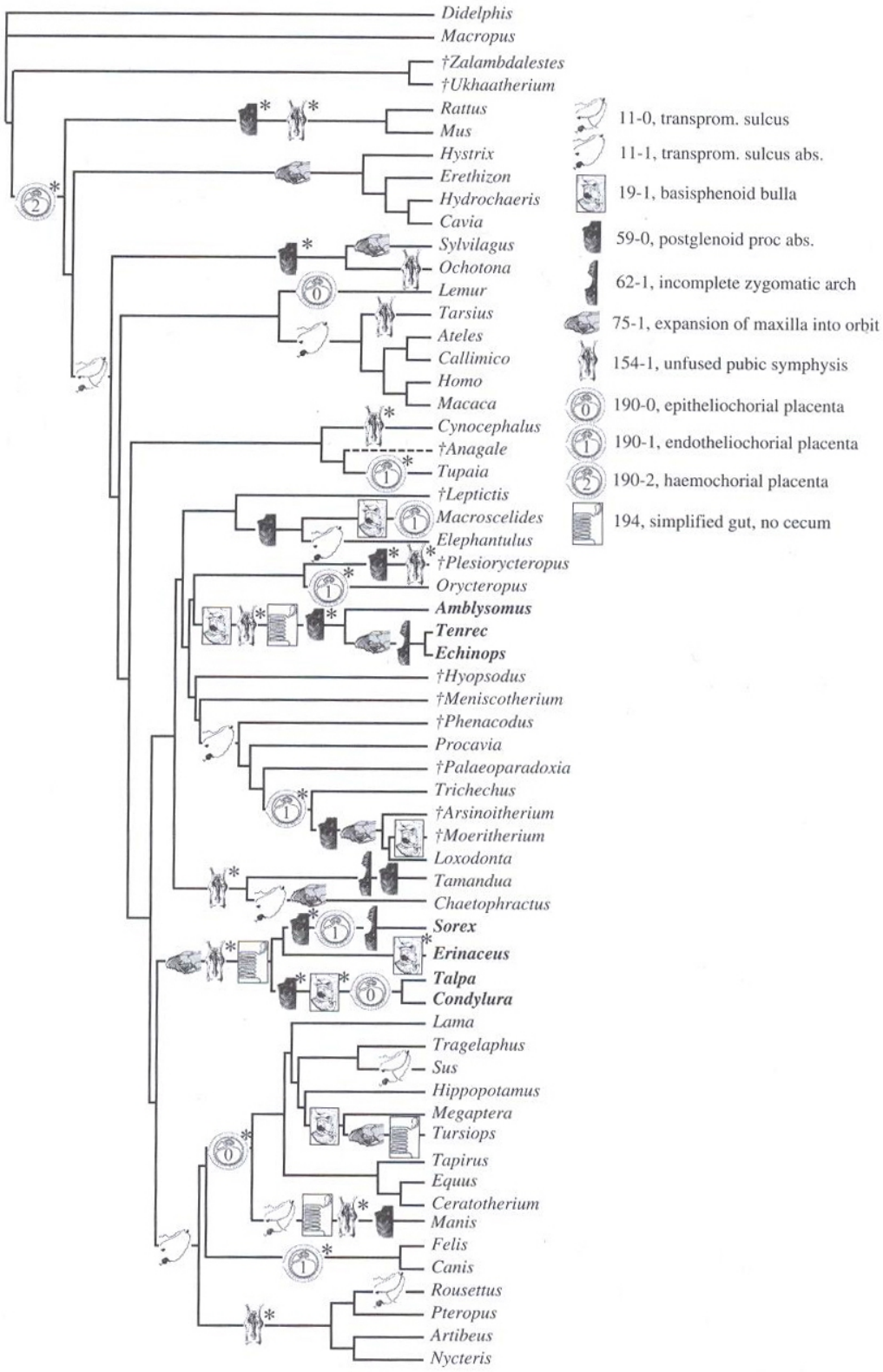


Figure 4.6—Cladogram from Asher (2005) showing Afrotheria as well as a monophyletic Eulipotyphla (*Sorex, Erinaceus, Talpa,* and *Condylura*).

Asher (2005, Figure 4.6) and Asher et al. (2005) published trees similar to Asher et al. (2003), but examined the effect of partitioning and removing subsets of the molecular data, even on fossil forms for which there is no molecular information. For example, *Leptictis* moved from being a sister-group to macroscelideans to falling near the leporids when certain subsets of the molecular data were removed from analysis.

Most recently, Beck et al. (2006) produced a supertree for placental mammals which, unusually, shows strong support for its higher level groupings, including Tenrecoidea as a part of Afrotheria, and a monophyletic Eulipotyphla. This may represent an emerging consensus on the position of the various modern "insectivores," but many questions remain regarding the fossil groups

iii. Conclusions

The taxonomic history of the Insectivora has been a long and convoluted one. The early history of the order was one of expansion, where a large number of diverse species, particularly macroscelidids, tupaiids, and dermopterans, and numerous fossil groups, were added to the original lipotyphlan core. These species were united only by generalized traits primitive for all Eutheria, and the Insectivora quickly became a wastebasket to house any fossil placentals which could not be clearly assigned to another order. This usage of the order was justified by the view that Insectivora included the basal eutherians, from which all other orders were derived; any eutherian not belonging to a derived order must be an insectivore. However, the precise relations within Insectivora, as well as the relationship of the order to other placental groups, were neither clear nor stable. Two main infra-ordinal divisions were suggested early on, the Menotyphla and Lipotyphla, based on the presence and absence of a caecum, and the Zalamdodonta and

Dilamdodonta, based on the structure of the upper molars; the two divisions were not fully compatible, and the compromise was usually to consider all Menotyphla “dilamdodont” and divide the Lipotyphla into dilamdodont and zalamdodont groups.

Beginning in the 1970s, the shift towards the cladistic method and an emphasis on monophyletic groupings united by synapomorphies led to the discarding of the notion of the “ancestral insectivore” (a paraphyletic concept), and an attempt to identify a monophyletic, derived Insectivora. This meant the removal of various groups that clearly had a long, independent history more deserving of separate ordinal status: the tupaiids, macroscelideans, and dermopterans, as well as fossil groups such as the apatemyids and leptictids. Some possible synapomorphies for the remaining “true insectivores,” the Lipotyphla, were identified: a reduced pubic symphysis, absence of a caecum, and a possibly distinctive arrangement of musculature of the snout.

The appearance of molecular phylogenies which included insectivores caused another major shift in the concept of the Insectivora, as they have consistently found Lipotyphla to be polyphyletic, with the Tenrecoidea (tenrecs + chrysochlorids) falling into the Afrotheria with elephants, hyraxes, sirenians, aardvarks, and macroscelidids. The remaining Eulipotyphla (shrews, hedgehogs, moles, and solenodons) are often but not always recovered as monophyletic. Although efforts to find morphological synapomorphies for the Afrotheria have not been fruitful, combined morphological-molecular studies, which were able to include fossil taxa, have supported Afrotheria as well as Eulipotyphla.

Although the molecular, cladistic method has produced new and interesting results, the details of the various cladograms which have been generated in the last ten years vary greatly. While we may continue to hope that larger, more taxonomically inclusive data-sets will improve

the consistency of the results and the support-strength of the various groups returned, to date the cladistic analyses have not produced a greater stability of phylogenies for the Insectivora than the traditional methods which came before them. Insectivore relations, both within the Eulipotyphla and to other mammals, remain uncertain and highly unstable.

For the purposes of this thesis, a simple classification based on the usage of Storer (1996) has been adopted. The term “insectivore” is used strictly as a casual or dietary descriptor for the groups studied in this project, and has no intended phylogenetic implications. The taxa under study are arranged into four orders, Lipotyphla (including Apatemyidae, Micropternodontidae, Geolabididae, Soricidae, and Oligoryctidae), Leptictida, Apatotheria, and Chiroptera. Only the Lipotyphla has multiple families clearly identified within it, although it is likely that the three chiropteran taxa do not all fall into the same family.

Chapter 5

Systematic Palaeontology

i. Chadronian Insectivores of the Cypress Hills

A diverse suite of insectivores is present in the Calf Creek and Horse Local Faunas. The individual taxonomic histories of these families is presented below.

Apatotheria

The Apatemyidae were first described by Marsh in 1872, who suggested they be considered insectivores, and were always a very distinctive group. Their confused history is reviewed by McKenna (1963), but at various times they have been considered insectivores, primates, and even rodents. For much of the period from the early 1900s to early 1930s they were considered synonymous with plesiadapids, most often as primates. Jepsen (1934) revived the family as a separate entity, tentatively within the Insectivora, but suggested the possibility that they should be placed in their own order, Apatotheria (Scott and Jepsen, 1936). Simpson still considered them to be primates (1945), while McKenna (1963) in his review placed them within Lipotyphla, and was followed by Van Valen (1967). They are absent from more recent classifications of insectivores. By 1975, McKenna (1975, McKenna and Bell 1997) changed his mind and classified them as the suborder Apatotheria in the order Cimolesta, with an assortment of other primitive mammals. Apatotherians have not been treated in any of the recent cladistic studies which have reshaped the insectivoran family tree.

Leptictis

Leidy (1868) described *Leptictis haydeni* and *Ictops* (now *Leptictis*) *acutidens*, ascribing them to the Insectivora as primitive relatives of the hedgehogs. This association with erinaceids was prevalent in the earlier literature (eg. Gregory, 1910; Simpson, 1945), although at other times they have been associated with tupaiids (McDowell, 1958; Van Valen, 1967). More recently they have been viewed as a separate group deserving classification of ordinal level or higher (McKenna, 1975; Butler 1988) although arguments for their re-inclusion in Lipotyphla have also been made (Novacek, 1986; MacPhee and Novacek, 1993). The most recent analyses including fossil forms, Asher et al. (2003, 2005) have tended to place them near Macroscelidea, though various partitioning of the molecular data in Asher et al. (2005) affect their position greatly: in one case inserting *Tupaia* between *Leptictis* and *Macroscelides*, and in another case leaving *Leptictis* closest to leporids and rodents.

Apternodus* and *Oligoryctes

These zalamdodont fossil taxa have been grouped together since the description of *Oligorcytes* by Hough (1956). *Apternodus* was described by Matthew (1903), who placed it in the Zalamdodonta but suggested no close affinities. This reticence with regard to intra-ordinal position has been followed by most subsequent workers, although Hough (1956) allied them with the Tenrecoidea. Butler (1972) included them tentatively within the Soricomorpha, then placed *Apternodus* with a question mark near the base of a *Nesophontes/Solenodon* clade (still not far removed from soricids) (Butler, 1988). McDowell (1958) had long ago critized the association between *Apternodus* and *Solenodon* and viewed *Apternodus* as unlikely to be closely related to any lipotyphlan, based on features of the skull. *Oligoryctes* appeared to be more typically lipotyphlan in its skull features (Hough, 1956; Asher et al. 2002), and the cladistic analyses of

Asher et al. (2002) did not support a familial grouping of the two. Rather, *Oligoryctes* fell closer to the shrews than to *Apternodus*, although both groups appeared to lie well within the core of the Lipotyphla.

Centetodon

The troubled taxonomic history of this genus was reviewed by Lillegraven et al. (1980), and involves several generic names, most notably *Metacodon* Clark 1936 and *Geolabis* Cope 1884. Like many fossil insectivores, the allocation of this genus within the order has been highly variable; often it has been placed in its own family, either as Centetidae (Matthew, 1909) or, more recently, Geolabididae (eg. McKenna, 1960; Butler, 1972). It has also been referred to the Leptictidae (Clark, 1936), Erinaceidae (Patterson and McGrew 1937), Nyctitheriidae (Romer, 1945), Metacodontidae (Butler, 1948), and Adapisoricidae (Romer, 1966; Van Valen 1967). The most recent analyses involving the taxon (Asher et al., 2002; 2005) place them near hedgehogs, and they are allied with the "core" Lipotyphlans in all permutations of the cladograms.

Micropternodus

This genus, described on the basis of a lower jaw fragment, was originally compared with tenrecs and placed among the Zalamdodonta (Matthew, 1903). Questions about this allocation were raised by McDowell (1958), and by 1960 Russell's review of the genus conclusively identified the dilamdodont uppers. A possible association of *Micropternodus* cranial material with the humeral genus *Cryptoryctes* was also discussed, an association which remains possible. Of the various genera which *Cryptoryctes* has been tentatively associated with, only *Micropternodus* is known to be present in the Calf Creek and Horse Local Faunas. Relationships with other lipotyphlan groups above the family level have not generally been examined for this

genus, though some have suggested similarities with talpids or proscalopids, particularly if the *Cryptoryctes* humeri are associated (Reed and Turnbull, 1965; Barnosky, 1981). The most recent analysis to include *Micropternodus*, Asher et al. (2002), placed it near erinaceids (either just above or unresolved with them) as the outgroup to all other insectivores.

Domnina

Domnina has been firmly classified as a shrew since the work of Patterson and McGrew (1937) identified the typically soricid upper molars, jaw structure, and tooth pigmentation of the genus. Before that it was poorly known from the lower dentition only, and was considered for some time to be a nomen dubium (Scott and Jepsen, 1936). This has made its phylogenetic position and classification history far more stable than most fossil insectivores. *Domnina* is assigned to the soricid subfamily Heterosoricinae, which includes early shrews of mid-Eocene to mid-Miocene age. Lopatin (2002, 2004) suggested a close relationship between nyctitheriids, an insectivore family known from the Paleocene to mid-Eocene in North America, and shrews and postulates the origin of shrews from nyctitheriids in the early to mid Eocene.

ii. Lipotyphla

1) Lipotyphla Haeckel 1866

Apternodontidae Matthew 1903

Apternodus Matthew 1903

Type species—*Apternodus mediaevus* Matthew, 1903

Referred species—

A. mediaevus Matthew, 1903

A. baladontus Asher et al., 2002

A. brevirostris Schlaikjer, 1934

A. gregoryi Schlaikjer,1933

A. iliffensis Galbreath, 1953

A. major Asher et al., 2002

A. dasophylakas Asher et al., 2002

Range (geographic and temporal)—Duchesnean through early Orellan throughout western North America.

Diagnosis—From Asher et al., 2002. "These insectivoran-grade mammals range in size from a large shrew (cf. *Crocidura*) to *Erinaceus*. Metacones are absent; talonids are reduced to a single cusp without a basin; and P4/p4 are molariform. The dental formula is 2.1.3.3/3.1.3.3, showing enlarged and procumbent upper and lower anterior incisors. The anterior margin of the coronoid process extends anteriorly to occlude part of m3 from lateral view."

Upper canine two-rooted, obtusely conical. Cheekteeth without interradicular crests

(From McDowell, 1958). P4 and M1-3 with simplified, zalamdodont tooth pattern. Protocone (see Fig. 5.1 and discussion for cusp homology) reduced to small cusp or shelf very low on lingual end of tooth. Pre- and postprotocrista join parastylule (anteriorly) and mesostyle (posteriorly). Major cusp of upper molar paracone, with parastyle and mesostyle situated lingually. i1 enlarged, i2 reduced. Lower cheek teeth (p4-m3) with typical trigonid; talonid reduced to a single, low cusp. m3 with lower trigonid than m1 and m2, talonid not elongate or raised as in *Oligoryctes*. Approximately 2X larger than *Oligoryctes*.

Discussion—Asher et al. (2002), in their detailed review of North American zalamdodonts, give an extensive but largely cranial diagnosis of the genus; only the portions relevant to the dentition have been quoted here. Additional dental characteristics are drawn from McDowell (1958) and personal observation. Asher et al. (2002) came to the conclusion, based upon occlusal relationships, that the main cusp of the zalamdodont upper molar is the paracone (Fig. 5.1). The author accepts their reasoning and follows their usage.

Apternodus sp., possibly *A. baladontus* Asher et al., 2002

Fig. 5.1, Plate I

Type specimen—FMNH UM1690, complete skull with both mandibles, McCarty's Mountain Local Fauna, late early Chadronian, Montana.

Referred specimens—

Calf Creek Locality:

Uppers: P661.479, LP4; P661.480, RM1, P661.481, RM1; ROM 23254, LM1; P1585.923, RM2;

Lowers: P1585.924, Rp4; P1585.928, Rm1 or 2; P661.482, Rm1 or 2; P1585.926, Lm1 or 2; P1585.930, Rm1 or 2; P1585.929, Rm1 or 2; P1585.927, Lm1 or 2; P1585.937, Rm1 or 2; P1585.925, Lm3; ROM 23255, Rm3.

Horse Locality:

Uppers: P2113.721, maxillary fragment with broken LM1; P2187.272, RM1; P2187.276, LM2; P2187.275, RM3;

Lowers: P2113.885, Rp2?; P2187.277, Rm1 or 2; P2113.720, Lm1 or 2; P2113.719, Rm3; P2187.273, Rm3.

Range (geographic and temporal)—Late Duchesnean to middle Chadronian of southwestern Montana (McCarty's Mountain 27, Diamond O Ranch 9, and Little Pipestone Creek 25), and perhaps Chadronian of southwest Saskatchewan.

Diagnosis—From Asher et al., 2002. "In addition to large, bulbous upper canines, bulbous i3-p3, and prominent molar protocones, *A. baladontus* shows a large, spherical upper P2 and I2, with P2 showing at least three and sometimes four roots (e.g., MPUM 2645). The upper canine has a prominent, buccally situated third root. The p3 lacks a prominent posterior cusp. *A. baladontus* is further distinguished from *A. mediaevus* by the small but distinct i2 which has an alveolus separate from that of i1, small cheek teeth with molars that show weak or absent buccal cingulids, the presence of a bony torus defining the ventrolateral margin of the external auditory meatus, and the ventrally short posttympanic process."

Description—

Upper teeth: typical of *Apternodus*. Upper molars are triangular and zalamdodont (Fig. 5.1, Plate I-A to D), with the protocone present as a ridge or small cusp set very low on the

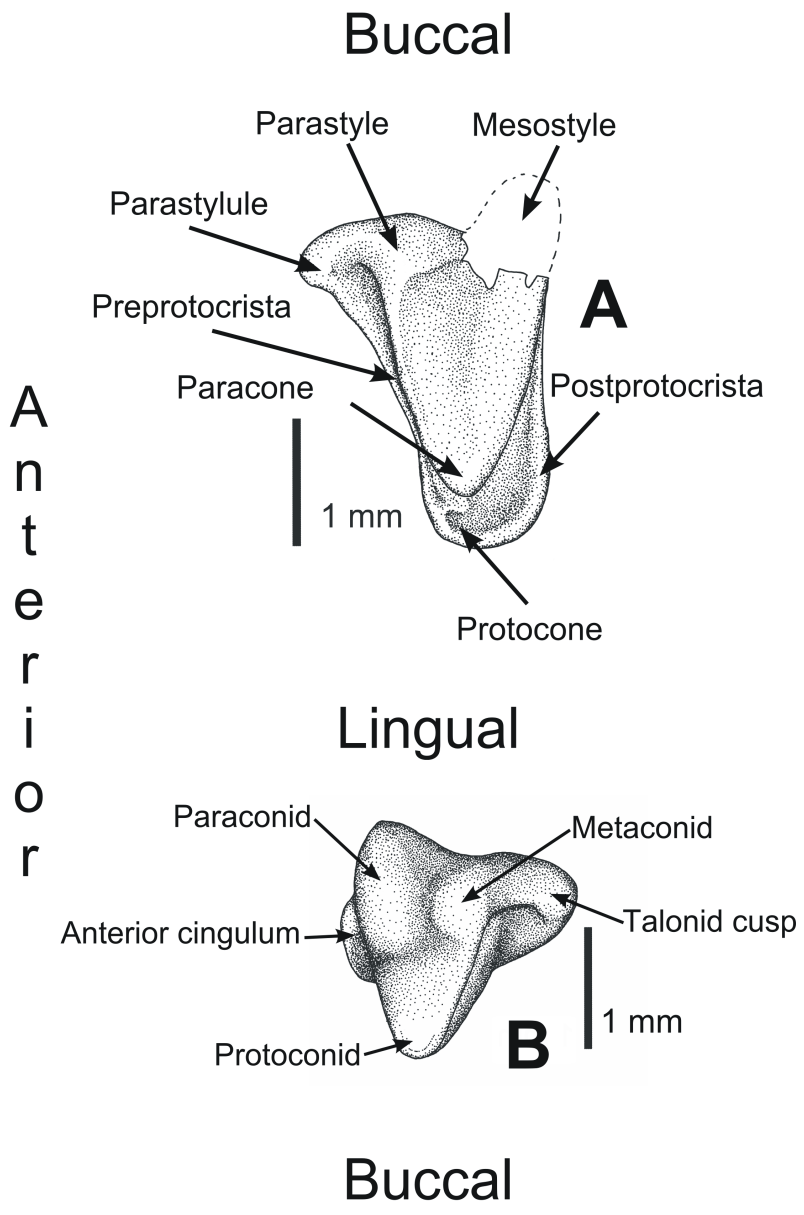


Figure 5.1—LM1 ROM 23254 and Rm1 or 2 P2187.277 (shown reversed).

lingual margin of the tooth (Plate I-C). Preprotocrista and postprotocrista run buccally up the sides of the crown; the preprotocrista joins the parastylule in a distinct hook on the anterior face of the tooth, while the post-protocrista ends either at the posterobuccal corner of the tooth or somewhat below it. The crown of the tooth is formed of three cusps, the paracone being the most lingual large cusp, and the two buccal cusps being a large parastyle and mesostyle. There is no stylar shelf beyond these two cusps.

P4: P4 is molariform, distinguishable from the M1 and M2 by its anteroposteriorly elongate shape (Plate I-A).

M1 and 2: In M1 (Plate I-B) the mesostyle extends further buccally, while in M2 the parastyle extends more buccally.

M3: M3 (Plate I-D), like P4, is anteroposteriorly elongate, but it is much narrower and

has a somewhat reduced mesostyle and postprotocrista.

p2: a single bulbous lower premolar, probably Rp2, has been recovered (P2113.885, Plate I-E and F). This is a procumbent, single-rooted tooth with an inflated, bulbous, and rather low crown. There is a distinct, although blunt, crest running along the anteroposterior axis of the tooth, suggesting it is somewhat less inflated than the premolars of other *Apternodus baladontus* specimens; however there is some variability in the exact shape of the bulbous premolars illustrated by Asher et al. (2002).

p4-m2: lower molars have a well-formed trigonid but reduced talonid (Fig. 5.1 bottom, Plate I-G and H). The protoconid is the highest cusp. A cingulum forms a subvertical ridge on the anterior face of the tooth, angling slightly buccad as it descends. p4 is molariform and p4 through m2 are essentially identical, varying only in the relative heights of paraconid and metaconid; the metaconid is very low in the p4. The talonid is basinless and reduced to a single cusp, much lower than the trigonid cusps, at the posterolingual corner of the tooth. The buccal surface of the molars is smooth, lacking a basal cingulum (Plate I-H).

m3: m3 has a shorter crown and even lower talonid cusp than the anterior molars; the talonid is longer than in m1 or 2 (Plate I-I).

Discussion—Asher et al. (2002) state that *Apternodus* species cannot be reliably diagnosed based on isolated molars alone. However, the current author felt that some effort should be made to narrow the field of species if possible.

With that in mind, the following observations were made: The Calf Creek specimens fall at the lower end of the size ranges for any *Apternodus* listed in Asher et al. (2002). This excludes larger-toothed species such as *A. major, A. gregoryi,* and *A. brevirostris* and likely *A. dasophylakas.* Overlap seems to occur chiefly with *A. baladontus, A. mediaevus,* and perhaps *A.*

iliffensis. The upper molar with the best-preserved protocone, ROM 23254 (Fig. 5.1, Plate I-B and C), from the Calf Creek, shows a protocone better developed than those in *A. iliffensis*. Other uppers are either broken above the protocone or do not show a protocone distinct from the lingual cingulum; however, these teeth are all somewhat waterworn, smoothing some of the surface details, which could obliterate the small protocone cusp. All upper molars from the Horse Locality are broken above the level of the protocone. The possible p2 described above is inflated and bulbous, but perhaps not to the same degree as the type material of *A. baladontus* or *A. mediaevus*. Lower molars from both sites lack buccal cingulids (Plate I-H), as in *A. baladontus* but unlike *A. mediaevus* and *A. iliffensis*. It thus seems likely that at least the majority of the *Apternodus* from the Calf Creek and the Horse Localities represent *A. baladontus,* but certainty cannot be achieved due to the fragmentary nature of the remains.

Apternodus baladontus is otherwise known only from south-western Montana, particularly the Pipestone Springs area. Geographically these localities are relatively close to the Cypress Hills, and many aspects of these faunas are shared, but some other Montana-specific species, such as *Centetodon kuenzii*, are not known from the Cypress Hills Chadronian. The other most likely possible identification for the Cypress Hills *Apternodus*, *A. mediaevus,* is also otherwise known only from SW Montana. *A. iliffensis* is known from Colorado, Wyoming, and Texas, and is the most widespread species of *Apternodus*.

Table 5.1—Measurements for *Apternodus* sp., possibly *A. baladontus.* All measurements are in mm. Mean and standard deviation (SD) are calculated where more than 3 measurements are available from one locality.

Specimen Number	Locality	Element	AP length	Ant width
P661.479	CC	LP4	2.6	>2.2
P661.480	CC	RM1	1.9	2.7
P661.481	CC	RM1	2.1	3.1
ROM 23254	CC	LM1	2.1	3.2
P2113.721	H	LM1	2.13	x
P2187.272	H	RM1	2.05	2.24
P1585.923	CC	RM2	1.8	>2.5
P2187.276	H	LM2	1.87	x
P2187.275	H	RM3	2.1	1.30
P2113.885	H	?Rp2	3.3	2.2
P1585.924	CC	Rp4	1.6	1.1
P661.482	CC	Rm1 or 2	1.8	1.5
P1585.926	CC	Lm1 or 2	2	1.6
P1585.927	CC	Lm1 or 2	2	1.5
P1585.928	CC	Rm1 or 2	>1.8	1.5
P1585.929	CC	Rm1 or 2	2.1	1.8
P1585.930	CC	Rm1 or 2	2.1	1.7
P1585.937	CC	Rm1 or 2	1.5	1.5
MEAN	**CC**	**m1 or 2**	**1.92**	**1.59**
SD	**CC**	**m1 or 2**	**0.23**	**0.12**
P2113.720	H	Lm1 or 2	x	1.24
P2187.277	H	Rm1 or 2	2.03	1.82
P1585.925	CC	Lm3	2	1.4
ROM 23255	CC	Rm3	1.8	1.5
P2113.719	H	Rm3	2.21	1.5
P2187.273	H	Rm3	1.86	1.39

2) Lipotyphla Haeckel 1866

Geolabididae Marsh 1872

Centetodon Marsh 1872

Type species—*Centetodon pulcher* Marsh 1872

Referred species—

C. magnus (Clark 1936)

C. hendryi Lillegraven et al. 1981

C. aztecus Lillegraven et al. 1981

C. chadronensis Lillegraven et al. 1981

C. bembicophagus Lillegraven et al. 1981

C. wolffi Lillegraven et al. 1981

C. marginalis (Cope, 1873) (Inc. *Geolabis rhynchaeus*)

C. kuenzii Lillegraven et al., 1983

Range (geographic and temporal)—Wasatchian to Arikareean of North America.

Diagnosis—from Patterson and McGrew (1937, for *Metacodon*). "P4 submolariform with parametacone, strong parastyle, metastyle crest. Upper molars narrow transversely, protoconules absent, metaconules absent or very small, external shelves wide with stylar cusps varyingly developed, parastyles strong, metastyle crest on M1-2, hypocone of M3 small. Lower C small, erect. p1 two rooted; p3 small in comparison with p2-4; p4 submolariform with metaconid not completely separated from, directly lingual to, and lower than protoconid; anterior cusp and talonid small, low. Trigonids of lower molars much higher than talonids, base of paraconid situated high on talonid. Horizontal ramus slender, shallow."

Discussion—The complex taxonomic history of *Centetodon*, including no less than five different generic names, was summarized by Lillegraven et al. (1981), and has been largely stable since that review. The diagnosis given for the genus by Lillegraven et al. (1981) is based on cranial features which are not available in the Cypress Hills material, so it has not been quoted here. The most complete dental diagnosis available comes from Patterson and McGrew (1937), which is quoted above. This is based on the diagnosis of Clark (1936), but included the upper dentition. To their diagnosis I would add the characteristic "twisted" appearance of the upper molars, where the protocone appears somewhat rotated in an anterior direction relative to the paracone and metacone, and the distinct, near-vertical anterior cingulum on the lower molars, which interlocks with the hypoconulid of the previous molar.

Centetodon chadronensis **Lillegraven et al.** 1981

Fig. 5.2, Plate II

Type specimen—USNM 181717, mandible with Lp1-4, Lm1-3 and pelvic fragments, Pipestone Springs Local Fauna, middle Chadronian of Montana.

Referred specimens—

Calf Creek Locality:

Uppers: P1585.959, RP3; P1585.958, LP4; P1585.961, RP4; P1585.960, RP4; P1585.962, RM1; P1585.963, LM1; P1585.964, LM1; P1585.965, RM1; P1585.966, RM1; ROM 23251, LM1; P1585.969, RM2; P1585.967, LM2; P1585.968, LM3; P1585.970, RM3.

Lowers: P1585.956, Rm1 or 2; P661.493, Rm1 or 2 (broken paraconid); P1585.898, Lm1 or

2; P1585.973, Lm1 or 2; P1585.972, Lm1 or 2; P1585.974, Rm1 or 2; P1585.975, Rm1 or 2; P1585.892, Rm3.

Horse Locality:

Uppers: P2113.764, LP3; P2113.779, LP4; P2187.283, LP4; P2187.256, RM1; P2113.754, RM1; P2187.282, RM1; P2187.291, LM1 (broken); P2113.748, RM3; P2113.755, RM1 or 2; P2113.752, LM1 or 2; P2113.753, LM1 or 2.

Lowers: P2113.772, Rm1 or 2; P2113.677, Lm1 or 2; P2187.254, Lm1 or 2; P2113.773, Rm1 or 2 (damaged trigonid); P2113.709, Lm1 or 2 (talonid only); P2113.783, Rm1 or 2 (talonid only); P2113.676, Lm3.

Range (geographic and temporal)—early to mid Chadronian of the White River Fm. Wyoming; early Chadronian of Chambers Tuff Formation (Vieja group), SW Texas; mid Chadronian at the Raben Ranch Locality of Nebraska; mid Chadronian of the Cypress Hills Formation, Saskatchewan.

Diagnosis—As in Lillegraven et al. (1981 and 1983). Only the portions relevant to the cheek dentition have been quoted.

"P3 three rooted with distinct protocone, paracone with rounded anterior border, no metacone, and is set sharply askew in jaw with anterior end canted anterolingually; P4 with paracone the tallest cusp of upper dentition, lacks metacone, has strong protocone but no conules or anterior basal cingulum, with strong posterior cingulum, and with undivided lingual root that is occasionally vertically grooved on lingual surface; upper tooth row constructed on two levels with antemolars set well dorsal to molars. P4 designed on "split-level" with anterior base set significantly more dorsal than posterior base; M1-3 distinctly transverse, with strong anterior and slightly stronger posterior lingual cingula that do not project beyond lingual extreme of the

protocone, broad stylar shelves, virtually nonexistent paraconule, rounded lingual base of paracone, weak metaconules, and four-rooted, with hypoconal root larger than and usually not strongly divergent from protoconal root... p4 semimolariform with strong metaconid, distinct paraconid, weakly developed labial cingulum, and talonid with pair of parallel ridges running anteroposteriorly along medial one-third; m1-3 moderately high-cusped and generalized... lacking a labial basal cingulum; m3 markedly smaller than m1-2; entoconid slightly weaker than other talonid cusps (especially in m3, in which it typically is a low elongate cusp aligned with edge of talonid crest), hypoconulid set closer to entoconid than to hypoconid, hypoconulid of m3 strongly protruberant to sharpened point, cristid obliqua usually slightly concave laterally and typically strikes trigonid at middle base of protoconid;"

Description—

Upper molar roots: The lingual roots of the upper molars of the Calf Creek and Horse *Centetodon* are separate, unlike the earlier Eocene species of the genus, although it is worth noting that one specimen, P1585.965 (Plate II-H), has incompletely separated roots, which are separate at the lingual margin but possess "wings" projecting buccally across the bottom of the tooth which join in a "v" shape. This buttressing extends about .8 mm below the base of enamel. Other specimens which preserve portions of the lingual roots do not show this connection. The roots appear to be more strongly divergent than is the case in *C. hendryi* and *C. magnus,* but not so flaring as those in the later *C. marginalis* and *C. wolffi*. They are typical of two Chadronian species of *Centetodon, C. chadronensis* and *C. kuenzii*.

P3: the P3 (Plate II-A, F) is triangular, with a prominent paracone. There are three cusps along the buccal margin, here referred to as parastyle, paracone, and metacone, and a small, low, protocone lingual to these. The middle cusp (paracone) is by far the highest, being tall and

somewhat conical with a posterior crest (postparacrista) extending to the metacone. The parastyle is low and conical and joins to the metacone by way of a buccal cingulum along the outer face of the paracone. The metacone is higher than the parastyle but lower than the paracone, and is visible mostly as a flattening of the postparacrista. The protocone is damaged in both Cypress Hills specimens, but would be the lowest cusp on the tooth, situated on the lingual and posterior side of the paracone.

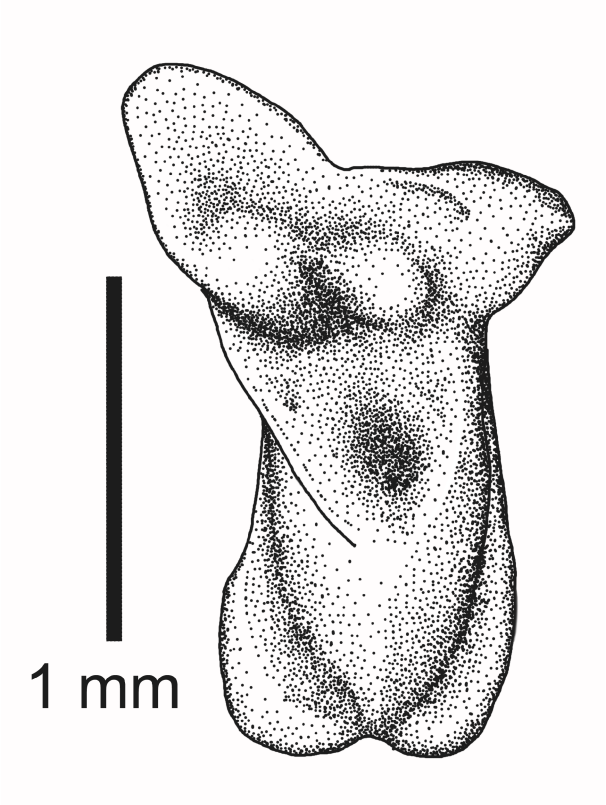


Figure 5.2—*Centetodon chadronensis* RM1 P1585.965, anterior to right. See Plate II-C for photograph.

P4: P4 is semimolariform (Plate II-B, G). The protocone is low and cuspate, positioned at the anterior edge of a lingual "heel." The paracone is high and sectorial, with a prominent postparacrista descending posterobuccally to the metacone, as in P3. Anterior to the paracone, the parastyle forms a small lobe on the anterobuccal margin of the tooth. In complete, unworn specimens it is a small but distinct cusp; in worn specimens it may be reduced to a shelf, and is often broken off. There may be a very narrow buccal cingulum. A small hypocone is present on the posterior margin of the lingual heel, joining a posterior cingulum, but there is only one lingual root. The P4s from the Horse Locality appear to be somewhat smaller than P4s from the Calf Creek, about 30% shorter and 10% narrower.

Upper molars: the upper molars have a conical paracone and metacone and a V-shaped protocone. There are no proto or metaconules, although a slight ridge and in some cases a

divergent protoloph or metaloph running to the paracone or metacone is present. The protocone is angled somewhat anteriorly, so that its cusp is in line with the paracone, giving the tooth a slightly twisted appearance. The central valley between the preprotocrista and postprotocrista is sharply defined, appearing pitlike in moderately worn specimens; in the gracile M3 specimen (P2113.748) this central pit actually perforates the tooth, although this may be pathological. A prominent crest (postmetacrista) trails from the metacone to the metastyle in M1 and M2. The stylar shelf is wide and bordered by a low ridge, but has few distinct conules. There is a prominent anterior shelf, sometimes almost as large as the small hypocone and talon which form a narrow shelf along the posterior margin of the tooth; both shelves extend from the level of the lingual margin of the paracone and metacone to the lingual end of the protocone, as in *Centetodon chadronensis*, but they do not meet and form a shelf around the lingual end of the protocone, as in *C. kuenzii*.

M1: M1 has a parastyle which forms a prominent lobe anterior to the paracone; the postmetacrista extends posterobuccad from the metacone and makes another prominent extension of the stylar shelf, directed posterobucally (Plate II-C, Fig. 5.2).

M2: the parastylar lobe of M2 is oriented buccally rather than anteriorly, and is larger than the metastylar lobe; the paracone has a preparacrista running buccaly into the parastylar lobe. The metastylar lobe is prominent with a sharp notch in the buccal face of the tooth between the two lobes (Plate II-D).

M3: M3 has a very enlarged parastylar lobe and a prominent preparacrista running buccally from the anterior of the paracone and joining the bulky parastyle. The metacone is smaller and positioned more lingually than in the other molars. The two M3s from the Calf Creek have relatively well-developed metacones with postmetacristae and metastylar lobes which curve

smoothly into the parastylar lobes; the M3 from the Horse lacks the postmetacrista and a metastylar lobe, and is somewhat smaller. This and the size-difference between the P4s are the only distinctive differences between the *Centetodon* uppers from the two sites. The anterior cingulum is small and low, while the hypocone and posterior cingulum are relatively large.

Lower molars: m1 and m2 are not readily distinguishable in isolated specimens; they are typically tribosphenic, with distinct, well-developed trigonid and talonid (Plate II-J). The most striking features are the anterior cingulum, which begins just buccal to the paraconid and descends sub-vertically towards the base of the anterobuccal corner of the tooth, and the hypoconulid, which projects posteriorly, in life fitting into the notch formed by the paraconid and anterior cingulum of the following tooth. In unworn specimens the hypoconulid is slender and curved. Molars lack a buccal cingulum, also as in *Centetodon chadronensis* (Plate II-L). One lower from the Horse Locality, P2187.254, is distinctly smaller (10-15%) than the other lower molars from that site, but still falls within the size range given for *C. chadronensis* by Lillegraven et al. (1983).

m3: m3 has a lower crown than the anterior molars, the talonid is narrower, and the entoconid is reduced, merging with the hypoconulid with moderate wear (Plate II-K).

Discussion—The form of the lingual roots of the upper molars is compatible with two *Centetodon* species: *C. chadronensis* or *C. kuenzii*. The uppers molars have anterior cingula and hypoconal shelves that reach the lingual end of the tooth but do not form a shelf across the lingual margin of the protocone, and the lower molars lack a buccal cingulum, indicating that the *Centetodon* from the Calf Creek and Horse Localities belong to *C. chadronensis*. Several teeth from the Horse Locality (M3 P2113.748, m1 or 2 P2187.254, m3 P2113.676) are smaller than other *Centetodon* teeth from the site, but still fall within the ranges reported by Lillegraven et al.

(1981) for *C. chadronensis.*

Table 5.2—Measurements of *Centetodon chadronensis*. All measurements are in mm. Mean and standard deviation (SD) are calculated where more than 3 measurements are available from one locality.

Specimen Number	Locality	Element	AP length	Ant width	Post width	LAH
P1585.959	CC	RP3	2.00	x	n/a	n/a
P2113.764	H	LP3	1.97	0.97	n/a	n/a
P2113.880	H	RP3	1.97	x	n/a	n/a
P1585.960	CC	RP4	>1.53	1.89	2.24	0.92
P1585.961	CC	RP4	1.87	1.73	2.24	0.87
P1585.958	CC	LP4	2.02	1.97	2.08	0.89
P2113.779	H	LP4	1.24	1.74	2.08	0.79
P2187.283	H	RP4	1.32	1.37	2.05	0.76
P1585.962	CC	RM1	>1.71	x	x	x
P1585.963	CC	LM1	1.89	2.34	2.58	1.11
P1585.964	CC	LM1	2.00	2.45	2.80	1.18
ROM 23251	CC	LM1	>1.23	>2.15	2.55	1.13
P1585.965	CC	RM1	1.95	2.67	3.00	1.31
P1585.966	CC	RM1	>1.29	2.37	x	1.11
Mean	**CC**	**M1**		**2.46**	**2.73**	**1.17**
SD	**CC**	**M1**		**0.15**	**0.21**	**0.08**
P2113.754	H	RM1	1.76	2.67	2.34	1.26
P2187.256	H	RM1	1.89	2.50	2.90	1.34
P2187.282	H	RM1	1.68	2.60	2.23	1.16
P2187.291	H	LM1	1.86	x	x	x
Mean	**H**	**M1**	**1.79**	**2.59**	**2.49**	**1.25**
SD	**H**	**M1**	**0.09**			
P1585.967	CC	LM2	1.50	2.82	2.76	1.05
P1585.969	CC	RM2	1.65	2.76	2.66	1.11
P2113.752	H	LM1 or 2	x	x	2.50	1.29
P2113.753	H	LM1 or 2	>1.34	x	2.45	1.50
P2113.755	H	RM1 or 2	x	x	2.26	1.18
P1585.968	CC	LM3	1.66	2.68	2.42	1.05
P1585.970	CC	LM3	1.60	2.73	2.47	1.05
P2113.748	H	RM3	1.23	2.26	1.50	0.87
						LOT
P1585.957	CC	Rm1 or 2	1.87	1.24	0.95	1.00
P1585.973	CC	Lm1 or 2	1.84	1.11	1.05	0.92
P1585.898	CC	Lm1 or 2	1.90	1.1	1.00	1.2
P1585.972	CC	Lm1 or 2	1.66	1.08	0.84	0.89
P1585.975	CC	Rm1 or 2	1.84	1.42	0.97	0.92
P661.493	CC	Rm1 or 2	>1.97	1.13	1.03	0.92
P1585.956	CC	Rm1 or 2	1.76	1.34	0.92	0.89
P1585.974	CC	Rm1 or 2	1.84	1.29	1.03	0.87
Mean	**CC**	**m1 or 2**	**1.82**	**1.21**	**0.97**	**0.95**
SD	**CC**	**m1 or 2**	**0.08**	**0.13**	**0.07**	**0.11**
P2113.772	H	Rm1 or 2	1.74	1.05	1.05	0.92
P2113.773	H	Rm1 or 2	>1.84	1.28	0.94	x
P2113.762	H	Lm1 or 2	1.89	1.08	0.86	0.87
P2113.677	H	Lm1 or 2	1.74	1.16	0.89	0.87

P2187.254	H	Lm1 or 2	1.50	0.97	0.74	0.74
P2113.709	H	Rm1 or 2	x	x	0.87	x
P2113.783	H	Rm1 or 2 talonid frag	x	x	x	x
Mean	**H**	**m1 or 2**	**1.72**	**1.07**	**0.88**	**0.85**
SD	**H**	**m1 or 2**	**0.16**	**0.08**	**0.11**	**0.08**
P1585.892	CC	Rm3	1.79	1.03	0.92	0.97
P2113.676	H	Lm3	1.42	0.87	0.66	0.73

3) Lipotyphla Haeckel 1866

Soricidae Fischer de Waldheim 1817

Heterosoricinae Viret and Zapfe 1951

Domnina Cope, 1873

Type species—*Domnina gradata* Cope, 1873

Referred species—

Domnina thompsoni Simpson, 1941

Domnina compressa Galbreath, 1953

Domnina greeni MacDonald, 1963

Range (geographic and temporal)—late Uintan of Saskatchewan (?), Chadronian of Nebraska and Saskatchewan, Orellan of Montana, Colorado, South Dakota, and Nebraska, through Arikareean of South Dakota.

Diagnosis—as given in Patterson and McGrew (1937). "I3/1, C0/0, P3/4, M3/3. Teeth heavily pigmented. P3 lacking. P4 with small protocone and hypocone. Upper molars with hypocones resembling those of *Blarina*, posterior cingula extending externally to metastyles. i3 less procumbent than in recent genera, without accessory cuspules, alveolar rim not extending posteriorily [original spelling] beneath premolars. p1-3 small; p1 larger than p2-3; p4 the largest of the series with single, conical, anteriorly projecting cusp and relatively strong transverse posterior cingulum. Lower molars progressively reduced in size from m1 to m3, protoconids and hypoconids sharply angulate externally, strong antero-external cingula; entoconids of m1-2 high, and connected by ridges to posterior slopes of metaconids. Talonid of m3 reduced, hypoconid small, entoconid greatly reduced or absent. Horizontal ramus heavy, deep, straight beneath

molars, mental foramen beneath m1."

Discussion—*Domnina* was described by Cope in 1873, but the holotype was fragmentary and the description vague; Scott and Jepsen (1936) viewed the genus as "of no importance," due to the lack of distinctive characteristics for the genus known at that time. The work of Patterson and McGrew (1937) identified the uppers, recognized the soricid affinities of *Domnina,* and established the modern definition of the genus.

Domnina thompsoni **Simpson, 1941**

Fig. 5.3, 5.4; Plate III

Type specimen—AMNH 32647, left lower jaw with alveoli of i2-p4, toothrow m1-3, most of postdental portion of jaw, from the middle Chadronian of the Pipestone Springs Locality, Montana.

Referred specimens—

Calf Creek Locality:

Lowers: P661.495, mandible fragment with Lm1 and 2; P1585.803, Rm2.

Horse Locality:

Uppers: P2113.729, RM1 or 2; P2113.730, LM1 or 2.

Lowers: P2431.005, mandible fragment with Lm1–3; P2113.784, Lm3; P2430.131, Rm2; P2187.264, Lm2; P2113.710, Rm2; P2113.711, Rm2; P2113.678, Lm1 or 2.

Range (geographic and temporal)—Chadronian of Pipestone Springs, Montana; Raben Ranch, Nebraska; and Cypress Hills, Saskatchewan.

Diagnosis—Based on discussions in Repenning (1967). Smaller than *D. gradata*, similar in size

to *D. compressa*. Premolars less crowded anteroposteriorly than other *Domnina* species; posterior root of p4 not transversely elongate or doubled. Molars not antero-posteriorly compressed as in *D. compressa.* Mental foramen situated under middle of m1.

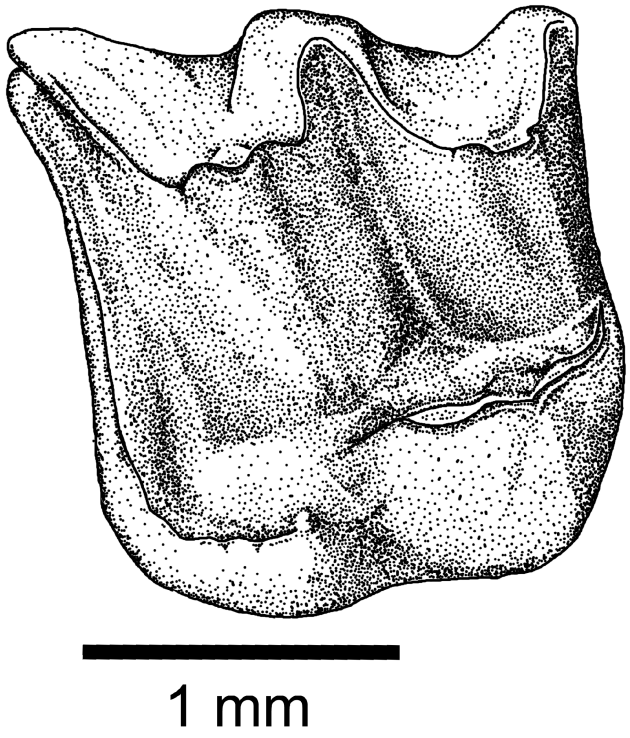


Figure 5.3—*Domnina thompsoni* RM1 or 2 P2113.729

Description—

Uppers: Two upper molars belonging to *Domnina* are known from the Horse locality; they are typical of the genus, with a strong W-shaped ectoloph connecting parastyle, paracone, mesostyle, metacone and metastyle (Fig. 5.3). The crescentic protocone is placed at the anterolingual corner of the tooth, with preprotocrista and postprotocrista running to the base of paracone and metacone respectively. The hypocone is a sharp, conical cusp posterior to the protocone and lingual to the metacone. An extremely well-developed, basined talon squares off the posterolingual corner of the tooth.

Lowers: The most complete *Domnina* specimen described here is P2431.005 (Figure 5.4, Plate III-A, B) from the Horse Locality, a fragment of mandible preserving pristine Lm1-3, as well as three closely-spaced alveoli anterior to the m1. The alveoli increase in size posteriorly, but the most posterior alveolus, while large, does not show any particular transverse broadening

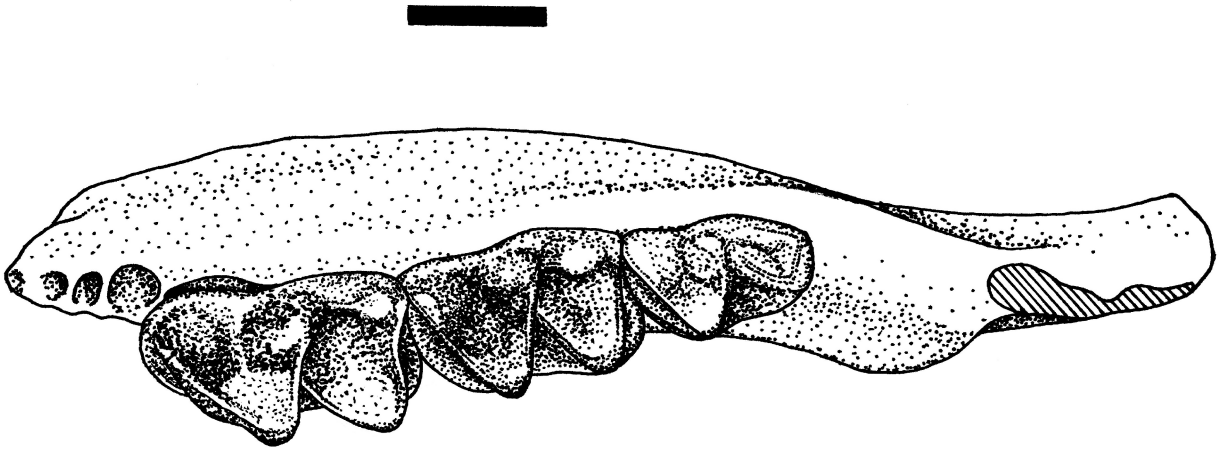


Figure 5.4—*Domnina thompsoni,* P2431.005, fragment of mandible showing Lm1-3.

or signs of doubling as in *D. gradata*. Molars are typically tritubercular, with a moderately high, triangular trigonid and a somewhat lower, also triangular talonid. m1 is the largest molar and m3 the smallest.

m1: the anterior portion of the buccal cingulum disappears as it reaches the posterior end of the trigonid, beginning again along the talonid. In P2431.005 the buccal cingulum is well-developed on all three teeth, but in P661.495 it is very faint in the m1. A similar condition was described by MacDonald (1963) in the Arikareean *D. greeni*, but this morphology is also visible in several specimens referred to *D. thompsoni* from the Pipestone Springs; it appears to be typical of *Domnina* m1s. The relevant portion of the m1 is damaged in the holotype of *D. thompsoni.* The paraconid and metaconid are widely-set and the paraconid is lower.

m2: in m2 the paraconid and metaconid are closer together and subequal in height. The highest cusp of the talonid is the entoconid, which is connected to the posterior surface of the metaconid by a distinct crest. The hypoconulid is lower, and has only a very slight "turn out" at the posterior of the tooth. The talonid and trigonid angle slightly anterad in parallel when viewed from the buccal side (Plate III-A).

m3: The trigonid of m3 is similar to m1 and m2, but the talonid is reduced to a small trapezoidal basin without distinct cusps.

Various specimens from the Calf Creek and Horse Localities, including teeth of *Domnina* as well as other teeth and bone from the sites, were examined under UV light to determine the nature of any fluorescence, since UV light has been used to detect traces of tooth pigmentation in other specimens of *Domnina* (Patterson and McGrew, 1937, Galbreath, 1953). However, no fluorescence of any kind was detected from any of the fossils from the Cypress Hills, in bone or dentine. Several elements in a bone-scrap sample from the Horse Locality did fluoresce brightly, but further inspection of these elements shows a different preservation than the bulk of the bone, and they appear to represent modern inclusions.

Discussion— The *Domnina* specimens from the Calf Creek and Horse localities appear to be generally somewhat smaller than the published measurements for *D. gradata*, although a few individuals overlap the *D. gradata* range. They are in most cases larger than the type of *D. thompsoni*, but plot well with specimens attributed to *D. thompsoni* from the Pipestone Springs area. The p4 alveolus preserved in P2431.005 is large but not transversely elongate or incipiently doubled, suggesting *D. thompsoni* rather than *D. gradata*. The Cypress Hills *Domnina* is not anteroposteriorly compressed and has a crest joining the entoconid to the metaconid, unlike *D. compressa.*

Table 5.3—Measurements for *Domnina thompsoni*. All measurements are in mm. Mean and standard deviation (SD) are calculated where more than 3 measurements are available from one locality.

Specimen Number	**Locality**	**Element**	**AP Length**	**Ant width**	**Post width**	**LAH**	**LBH**
P2113.729	H	RM1 or 2	1.89	1.89	2.11	1.76	1.71
P2113.730	H	LM1 or 2	1.71	1.76	>1.76	1.60	x
						Trigonid length	
P661.495	CC	Lm1	1.89	1.05	1.18	1.11	
P1585.803	CC	Rm1	2.15	1.37	1.26	1.24	
P2431.005	H	Lm1	2.00	1.18	1.32	0.92	
P661.495	CC	Lm2	1.79	1.00	1.05	1.05	
P2431.005	H	Lm2	1.79	1.13	1.13	0.79	
P2430.131	H	Rm2	1.97	1.36	1.39		
P2187.264	H	Lm2	1.74	1.32	1.29	0.74	
P2113.710	H	Rm2	1.84	1.13	1.05	0.89	
P2113.711	H	Rm2	1.84	1.08	1.13	0.86	
Mean	**H**	**m2**	**1.84**	**1.20**	**1.20**	**0.82**	
SD	**H**	**m2**	**0.08**	**0.14**	**0.14**	**0.07**	
P2113.678	H	Lm1 or 2	x	x	0.97	x	
P2431.005	H	Lm3	1.58	0.84	0.47	0.60	
P2113.784	H	Lm3	1.47	0.92	0.52		

4) Lipotyphla Haeckel 1866

Micropternodontidae Stirton and Rensberger 1964

Micropternodus Matthew 1903

Type species—*Micropternodus borealis* Matthew, 1903

Referred species—

M. strophensis (White, 1954)

M. morgani Stirton and Rensberger, 1964

M. montrosensis Ostrander 1983

Range (geographic and temporal)—Uintan? to Arikareean of North America; early Paleocene to mid Eocene of Asia, early Eocene of Europe.

Diagnosis—(abbreviated and highly modified from Stirton and Rensberger, 1964)

Three upper incisors, I1 greatly enlarged in *M. borealis*, not known in other species. Canines with one root. P1 not present. P2 minute or absent. P3 nearly triangular; main cusp an oblique sectorial blade with steeply inclined posterior edge. P4 submolariform; paracone high, sectorial; talon shelf much as in molars.

Molars with large, well developed hypocones and talons forming a broad shelf from the lingual margin of the tooth to level of metacone or beyond. M1with somewhat conical, appressed paracone and metacone, weak ectoloph. M2 with strongly W-shaped ectoloph, crescentic paracone and metacone.

Alveolus for i2 larger than those for i1 and i3. Canine alveolus apparently for one root. p3 much larger than p2, somewhat submolariform. p4 and lower molars with very high and anteroposteriorly narrow trigonids, with upper half of crowns curving posteriorly; talonids equal

to or narrower than trigonids and about half as high or higher; anterior spur of hypoconid connecting on posterior surface of protolophid at midline of tooth on lower molars.

Smaller than *Clinopternodus;* lower canine, crowns of p3, p4, m1 not as procumbent nor lingually curved, tips of crowns more recumbent than in *Clinopternodus;* p2 present although small; p3 higher crowned than in *Clinopternodus;* m1 talonid almost equal to height of trigonid.

Micropternodus strophensis (White 1954)

Fig. 5.6; Plate IV

Type specimen—USNM 18870, rostrum with cheek teeth, Canyon Ferry Local Fauna, middle Chadronian, Montana.

Referred specimens—

Calf Creek Locality:

Uppers: P661.494, RM1; P1585.976, LM1; P1585.940, LM2; P1585.942, RM2.

Lowers: P1585.943, Lp4; P1585.944, Rp4; P1585.1044 Lp4; P1585.945, Lm1; P1585.947 Lm1; P1585.950, Lm1; P1585.953, Lm1; P1585.948, Lm2; P1585.949, Lm2; P1585.951, Rm2; P1585.946, Lm1 or 2; P1585.952 Rm1 or 2; P1585.954, Rm3; P1595.955, Rm3.

Horse Locality**:**

Uppers: P2113.735, RP4; P2430.134 RM2; P2113.733, RM2; P2113.750, RM3.

Lowers: P2113.776, Rp4; P2113.728, Lm1; P2113.774, Rm1; P2113.775, Lm1; P2113.780, Rm1; P2113.732, Rm2; P2113.734, Rm2; P2113.736, Lm2; P2113.777, Lm3.

Range (geographic and temporal)—Chadronian of Montana, Wyoming, Nebraska, and Saskatchewan to Earliest Arikareean of Oregon.

Diagnosis—(based on differences noted within the text of Stirton and Rensberger, 1964, and Ostrander, 1987, and personal observation)

Smaller than *Micropternodus montrosensis,* same size as *M. borealis* and *M. morgani.* Rostrum wider than in *M. borealis,* narrower than *M. morgani*. Dentition lower-crowned than *M. morgani*, similar to *M. borealis*. Sectorial blade of P4 less oblique (Fig. 5.5-A, B) than in *M. borealis*, more oblique than *M. morgani*. Concavity on buccal surface of P4 shallower and wider than in *M. borealis*, more concave than *M. morgani*, lacking flattened buccal cingulum between paracone and metacone on *M. morgani*. "Hooklike" metastylule on P4. M1 preprotocrista forms complete connection to parastyle, unlike *M. borealis* or *M. morgani* where preprotocrista ends at paracone. Parastyle and metastyle on M1 less prominent than in *M. borealis*. Talon less extensive buccally than *M. morgani,* ending at lingual edge of the metacone, not buccal edge as in *M. morgani*.

Lower molars more recumbent than in *M. borealis.* Height of talonid more than half trigonid in unworn specimens. Buccal shelf between base of protoconid and hypoconid minute or

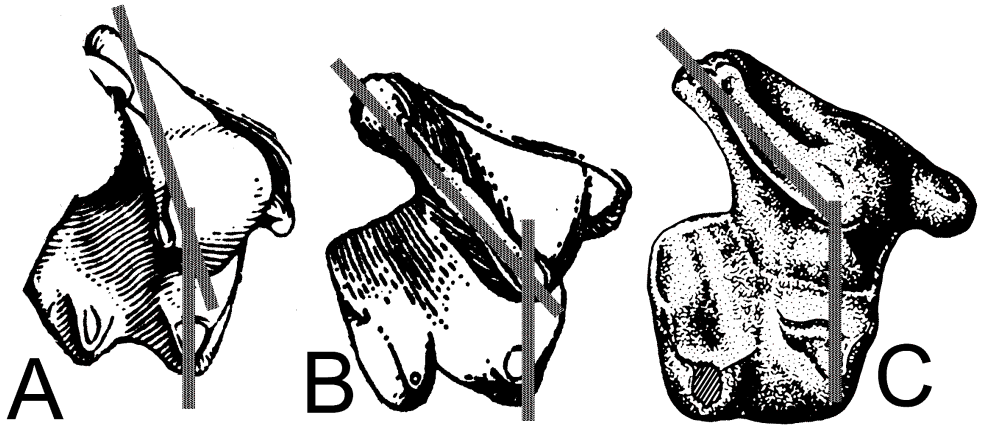


Figure 5.5—Orientations of sectorial blade in RP4 of *Micropternodus borealis* (A), *M. strophensis* (B), and P2113.735 (C). Anterior to right.A from Russell, 1960; B from White, 1954.

absent.

Description—

P4: No P4s have been identified from the Calf Creek Local Fauna. One P4, P2113.735, is identified from the Horse Local Fauna (Fig. 5.6-A). It is semi-molariform, with a prominent, blade-like paracone (Plate IV-A). The posterior face of the paracone slopes down in a crest to the location of the metacone, which is marked only by a flattening of the angle of descent, before a sharp drop to the metastyle; this paracone-metacone crest forms the sectorial blade (Plate IV-B). The sectorial blade is at an angle of about 135° (Fig. 5.5-B) to a line drawn through the protocone and paracone, making it similar in orientation to the blade of *M. strophensis* (140°, Fig. 5.5-B) and considerably less oblique than that of *M. borealis* (160°, Fig. 5.5-A). There is a well-developed parastyle. A narrow cingulum is present on the buccal surface, beginning at the base of the parastyle and running across the tooth to the middle of the concavity posterior to the paracone. This may be similar to, but less developed than, the structure described by Stirton and Rensberger (1964) for *M. morgani*. The protocone is a narrow, V-shaped cusp with poorly-developed protoloph (preprotocrista) and metaloph (postprotocrista). Hypocone and talon are well-developed. A minute crest connects the hypocone to the protocone anteriorly, while another curves posteriorly from the hypocone and forms the low margin of the talon. The talon ends buccaly near the lingual margin of the paracone, forming a right angle with the posterior margin of the trigon. P4 crown height is 2.2 mm, comparable to that of *M. borealis* (estimated 2.2 mm) and *M. strophensis,* (2.2 and 2.1 mm on the right and left sides of USNM 18870, respectively) much lower than the crown height of the P4 of *M. morgani* (3.7 mm, Stirton and Rensberger, 1964).

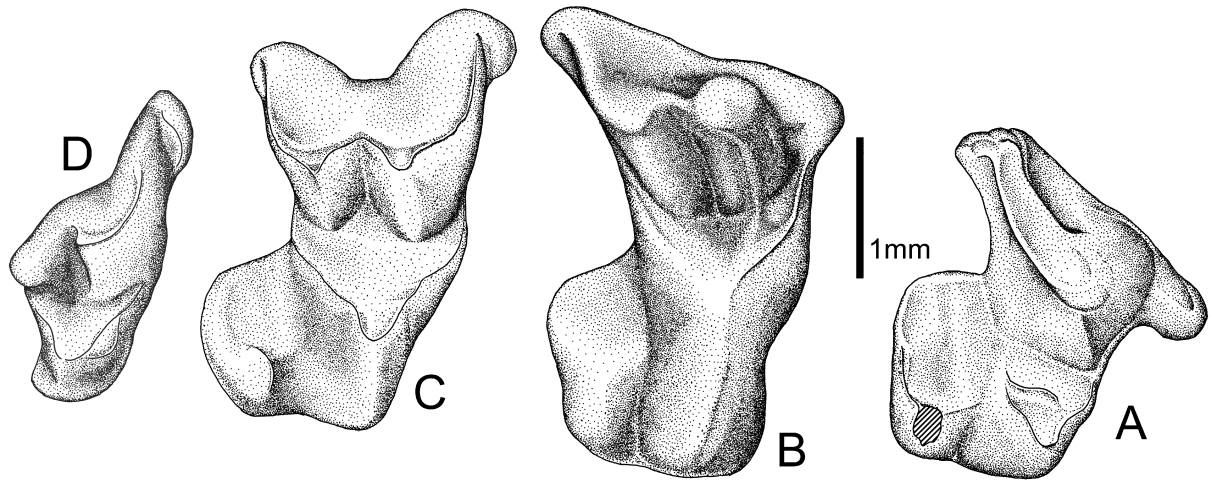


Figure 5.6—Micropternodus uppers from the Cypress Hills; anterior to right. A, RP4 P2113.735; B, RM1 P661.494; C, RM2 P2113.733, D, RM3 P2113.750.

M1: Two M1s are known from the Calf Creek Locality (Fig. 5.6-B); none are known from the Horse Locality. The paracone and metacone are high, conical cusps situated very close together on the tooth. They are united for most of their height, being separated only by a shallow valley near their apices. A short preparacrista runs down to the low parastyle. The preprotocrista (protoloph of Stirton and Rensberger) runs along the anterior base of the paracone to join the parastyle. The postparacrista and premetacrista are very poorly developed, and there is no mesostyle. The postmetacrista runs to a high, hook-shaped metastyle. The buccal face of the tooth is largely smooth, with a narrow cingulum connecting parastyle and metastyle and a slight concavity between metacone and metastyle. The protocone is a v-shaped, crescentic cusp, rather anteriorly-directed (procumbent), lower than the paracone and metacone. The hypocone is a ridge-shaped cusp on an extensive talon; a low crest from the posterior of the hypocone forms the posterior edge of the talon. The talon extends to the lingual edge of the paracone and metacone, and rejoins the trigon at an almost right angle.

M2: M2s are known from both Calf Creek and Horse Localities. The chief distinction between M1s and M2s is the appearance of the paracone and metacone. In M1, they are relatively conical cusps; in M2 they are crescentic and v-shaped, forming a well-developed, W-shaped ectoloph. The preparacrista connects to a hook-shaped parastyle. The postparacrista and premetacrista angle buccally to join at the middle point of the "W", the "mesostyle," which takes the form of a vertical ridge along the buccal surface of the tooth, although one specimen, P1585.942 (Fig. 5.6-C), has no mesostylar ridge at all, and the buccal surface of the tooth has a smooth, concave profile, rather than the more typical double-concavities formed by the two halves of the "W." The condition of the mesostyle is unclear as it is worn or damaged in all specimens. The protocone is similar to that of M1, but the preprotocrista ends at the paracone. The hypocone and talon are similar to M1; the angle at which the buccal rim of the talon contacts the trigon is somewhat variable, from an approximately right angle to a somewhat more obtuse one.

M3: The M3 referred to *M. strophensis* from the Horse Locality, P2113.750 (Fig. 5.6-D), is a triangular tooth smaller than any of the M1s or M2s. It has a well-developed, hook-shaped parastyle and crescentic, V-shaped paracone as in the M2, but the metacone is reduced to a small, conical cusp posterolingual to the paracone. Unlike the holotype of *M. strophensis,* there is a very small talon present as a low shelf on the posterior margin of the protocone. There is no hypocone.

p4: The fourth premolar is semi-molariform (Plate IV-C, G). The paraconid is present as a small, spiky cusp very low on the anterior face of the tooth, with a cingulum running down the buccal surface and along the base of the crown below the protoconid. The protoconid and metaconid are much higher, and are conjoined for much of their height. The tip of the metaconid is lower than the protoconid. The talonid has one large cusp, the hypoconid, located

approximately in line with the groove between protoconid and metaconid, at a height similar to the paraconid. A low crest spans the gap between the posterior face of the trigon and this talonid cusp. The buccal cingulum runs from the paraconid down and along the base of the crown, and back up to the hypoconid; it is interrupted midway along this path by the base of the protoconid. The least worn specimens, P2113.776 and P1585.1044, preserve another minute cuspule lingual to the main talonid cusp; the other p4 specimens show only a ridge in this position. A low crest runs anteriorly from the ridge/cuspule back to the trigonid, enclosing a very small talonid basin.

m1: Trigonids are tall and curved, bowing anteriorly. The paraconid is very low on the front of the tooth, mostly represented as a leveling out of the crest which runs steeply down the anterior face of the tooth from the protoconid (Plate IV-D, H). In most specimens a short anterior cingulum runs up and lingually towards the paraconid but does not reach it; some specimens lack this cingulum and have smooth anterior surfaces below the paraconid. The protoconid is the largest cusp but the metaconid is only slightly lower in height. The crest which joins the protoconid and metaconid has a v-shaped profile in anterior view. Wear can reduce the height of the protoconid and metaconid considerably, to the height of the paraconid and below, creating a smoothly-curved surface to the trigonid, with slight rises at the lingual and buccal edges. The talonid is very low, half to just over half the height of the trigonid. The hypoconid is the largest cusp, visible chiefly as the apex of the crest rimming the buccal margin of the talonid. On unworn specimens a small hypoconulid and minute entoconid are visible on the posterior margin of the talonid. In moderately worn specimens the entoconid vanishes, but the hypoconid remains visible as an irregularity in the outline of the talonid. In heavily worn specimens only a smooth ridge forming the posterior margin of the talonid is visible. There is no buccal or posterior cingulum, although in the Calf Creek Locality specimens of m1 and m2 a narrow shelf is present

between the base of the protoconid and hypoconid (Plate IV-I). This ridge is generally absent in the Horse Locality specimens. This shelf is the only consistent difference between the *Micropternodus* lower molars from the two sites, and though it may represent a temporal variation, seems vastly insuffi cient on its own to distinguish a new species.

m2: The most striking difference from m1 is in the paraconid, which is high and subequal to the metaconid, creating an almost symmetrical trigonid (Plate IV-E, I). Although still convex, the trigonid is less bowed anteriorly, and worn specimens may appear almost straight. Other features are the same as in the m1.

m3: m3 is somewhat smaller than the anterior molars. It is lower-crowned, and the trigonid is essentially straight rather than bowed anteriorly. The trigonid is similar to m2, though somewhat smaller, with paraconid, metaconid, and protoconid of subequal height. The talonid is narrower than in the anterior molars, and shows two subequal cusps (hypoconid and entoconid?) set close together, each connected to the posterior face of the metaconid by a low, straight crest. This creates a narrow, closed, roughly rectangular talonid basin.

Discussion—Russell (1960), in describing the upper dentition of *Micropternodus,* synonymized *Kentrogomphios strophensis* White 1954 with *Micropternodus borealis.* Stirton and Rensberger (1964) noted a number of minor differences between the types of the two species, summarized in the diagnosis above, and revived *Micropternodus strophensis*. However, many of these characteristics are very minor or subjective, such as the concavity on the buccal surface of the P4 or the recumbency of the lower molars.

Ostrander (1987) used three of these characteristics to distinguish *Micropternodus strophensis* from *M. borealis*. These were: "1) the dentition of *M. strophensis* is less cuspate than that of *M. borealis*, the cusps and crests having become more blade-like, especially on the

upper molars; 2) P4 is more molariform in *M. strophensis*; and 3) the protoloph connection to the parastyle is discontinuous in *M. borealis*."

Personal observation of the type of *M. strophensis,* USNM 18879, and a cast of the described uppers for *M. borealis*, CM 8674, does not support Ostrander's first distinction. The second observation is unclear, since the basic semi-molariform character of the P4 is the same in both species: prominent paracone as part of a sectorial blade, small metacone not distinct from the blade, narrow protocone, well-developed hypocone and talonid. Stirton and Rensberger elaborated their initial comment on the P4's molarification with a dicussion of the orientation of the sectorial blade of the P4 (formed between the paracone and the rudimentary metacone) and a description of the concavity of the buccal surface in the P4s of *M. strophensis* and *M. borealis.* The orientation of the sectorial blade has been measured here by drawing an imaginary line between the paracone and protocone and measuring the angle of the blade relative to this line; in *M. borealis* this angle is around 165°, interpreted as a more oblique orientation of the blade relative to the toothrow, while the angle in *M. strophensis,* around 140°*,* indicates a less oblique orientation to the blade. The difference in the breadth and depth of the buccal concavity is visible on the P4s, but is a very minor character and examination of more specimens should be undertaken to confirm its taxonomic usefulness. Ostrander's third point, the connection of the protoloph (preprotocrista) to the parastyle is valid, but only applies, as Stirton and Rensberger (1964) noted, to the M1. The M2's protoloph does not connect to the parastyle in either *M. borealis* or *M. strophensis*.

Stirton and Rensberger (1964) note very few differences between the lowers of *M. borealis* and *M. strophensis;* Ostrander (1987) says that the lowers are essentially similar. One of the differences suggested by Stirton and Rensberger is in the height of the talonid relative to the

trigonid: they say that the talonid in *M. borealis* is around half the height of the trigonid, while in *M. strophensis* it is slightly more than half. This character is somewhat difficult to evaluate since ratios of talonid to trigonid height vary based on the wear of the tooth, with trigonids being lower relative to talonids in worn specimens, not to mention depending on the angle at which the tooth is measured. However, allowing for these difficulties, even the least-worn specimens from the Horse and Calf Creek Localities have talonids more than half the height of their trigonids, when measured from a line perpendicular to a line through the tip and base of the trigonid (Plate IV-I). Stirton and Rensberger also identify a buccal shelf connecting the base of the hypoconid to the base of the protoconid in *M. borealis* but not in *M. strophensis;* however, a small shelf is present in the *M. strophensis* paratype lowers (USNM 18871), joining the buccal margins of the protoconid and hypoconid on the m2. A similar small crest is present in the Calf Creek specimens, but is generally absent in the Horse Locality specimens. Unfortunately the author has not personally observed the state of this character in the type of *M. borealis,* so cannot describe how it is different from that in *M. strophensis*. However, the state present in the Calf Creek specimens is similar to that in *M. strophensis*, and if the shelf is more developed in *M. borealis* then the Horse specimens would definitely not conform to the morphology of *M. borealis*.

Micropternodus borealis and *M. strophensis* are very similar, and studies of larger populations may eventually determine that intraspecific variation can encompass both species, since the most detailed examination of the two to date, Stirton and Rensberger (1964), was based on the type material alone for the two species. Possible distinctions favoured here are: 1) orientation of the sectorial blade of P4; 2) continuity of the preprotocrista (protoloph) with the parastyle in M1 in *M. strophensis,* discontinuity in *M. borealis*; 3) height of the trigonids relative to the talonids, particularly in m1 and m2 (trigonids > ½ height of talonid in *M. strophensis*,

about ½ height in *M. borealis*); and possibly 4) development of a labial shelf connecting the base of the protoconid and hypoconid in m1 and m2 (slight in *M. strophensis*, well-developed in *M. borealis*). The first characteristic refers the Horse Locality *Micropternodus* to *M. strophensis.* The second does the same for the Calf Creek *Micropternodus.* The characteristics of the lowers are more ambiguous, as discussed above, but still seem to lean in the direction of a referral to *M. strophensis* for the specimens from both the Calf Creek and Horse Localities based on the third distinction, talonid height. However, certain differences have been noted which might suggest a potentially different species at the Horse locality: sectorial blade of the P4 even less oblique than in *M. strophensis;* presence of a minute talon on the M3; and the lack of even a small shelf between the protoconid and hypoconid on the buccal face of the lower molars. The M2 from the Calf Creek which lacks a mesostyle, P2113.733, also represents a variation from the morphology of the holotypes of *M. borealis* and *M. strophensis.* On the whole, however, these variations are subtle and do not form a compelling pattern for the basis of a new species, particularly given the small numbers of specimens concerned.

Micropternodus cf. *M. montrosensis* Ostrander 1983

Plate V-A

Type specimen—USNM 18870, lower fragment jaw with p4-m1, Raben Ranch Local Fauna, middle Chadronian, Nebraska.

Referred specimens—

Calf Creek Locality: P1585.983, LP4; P1585.941, RM2; P1585.977, LM1 or 2.

Range (geographic and temporal): middle Chadronian of Nebraska, Saskatchewan.

Diagnosis—From Ostrander (1983), p. 129. “Largest known species of the genus; heel of p4 with entoconid but no other cusps; lower molars with long and prominent anterior cingulum, carnassial notch, and a small hypoconulid positioned lingually.”

Description—Three upper cheek teeth attributable to *Micropternodus* appear to be significantly larger than the others from the Calf Creek locality. Two specimens, P1585.983 and P1585.977, are badly broken, preserving only part of the protocone and the typical morphology of hypocone and talon, but they are much larger than other *Micropternodus* from the locality. The narrowness of the protocone in P1585.983 suggests that the tooth is likely a P4. The third specimen is complete and has the typical appearance of an upper 2nd molar of *Micropternodus* (Plate V-A), but it is significantly larger, about 6% in width and 20% in length (talonid included) than the largest dimensions for M2s reported for *M. borealis* (Ostrander, 1987), and is almost 40% longer and 20% wider than other Cypress Hills specimens. It has a V-shaped, subequal paracone and metacone forming a well-developed, W-shaped ectoloph. The preparacrista extends forward to the parastyle,with a low, hook-shaped parastylule. The mesostyle forms a vertical ridge along the buccal surface of the tooth. The metastyle is damaged. The protocone is also V-shaped, larger than the metacone and paracone. The preprotocrista has a small protoconule and extends forward to the anterior face of the paracone, but does not connect with the parastyle/parastylule. The hypocone and talon are very well developed. The hypocone occupies the lingual portion of the talon and has a low crest connecting it anteriorly with the side of the postprotocrista, dividing the basin of the talon into two: a short, deep valley open to the lingual margin of the tooth, and a larger but shallow basin on the buccal side of the hypocone. A low crest runs along the posterior rim of the talon, beginning posterior to (but not connecting with) the hypocone and continuing around the curve of the talon back towards the trigon. In the area adjacent to the trigon slight

wear has obliterated the ridge. The buccal margin of the talon meets the trigon at a level with the mesostyle, but the posterior portion of the talon is damaged and the original extent may have been even greater.

Discussion—Ostrander (1983) described the lowers of *M. montrosensis* from the Chadronian-aged Raben Ranch Local Fauna in Nebraska. The most striking characteristic of the species is its large size, having molars 10% to 40% longer than other *Micropternodus* species. Although no lowers referable to *M. montrosensis* were found at the Calf Creek Locality, the size of these uppers appears to be compatible with the lowers described by Ostrander, and in the absence of evidence to the contrary it seems reasonable to suggest that they represent upper cheekteeth of *M. montrosensis*.

Table 5.4—Measurements for *Micropternodus*. All measurements are in mm. Mean and standard deviation (SD) are calculated where more than 3 measurements are available from one locality. Trigonid and talonid height are recorded only in unworn lower molars. AP length does not include hypocone.

Specimen number	Species	Locality	Element	AP length	Ant width	Post width	LAH	LBH
P2113.735	*M. strophensis*	H	P4	2.24	2.16	2.39	1.58	1.08
P1585.976	*M. strophensis*	CC	LM1	>1.3	3.00	>2.6	2.10	1.40
P661.494	*M. strophensis*	CC	RM1	2.30	3.10	2.80	2.20	1.60
P1585.940	*M. strophensis*	CC	LM2	>1.70	>1.5	>1.5	2.00	1.40
P1585.942	*M. strophensis*	CC	RM2	>2.00	>2.3	3.10	1.70	1.40
P2430.134	*M. strophensis*	H	RM2	x	x	2.89	1.71	1.32
P2113.733	*M. strophensis*	H	RM2	1.89	3.00	2.70	2.16	1.37
P2113.750	*M. strophensis*	H	RM3	1.50	2.37	1.39	0.76	0.87
							Trig. height	**Tal. height**
P1585.1044	*M. strophensis*	CC	Lp4	1.73	0.97	0.94		
P1585.943	*M. strophensis*	CC	Lp4	1.66	1.21	1.00		
P1585.944	*M. strophensis*	CC	Rp4	1.76	0.92	0.73		
P2113.776	*M. strophensis*	H	Rp4	1.66	0.89	0.84		
P1585.945	*M. strophensis*	CC	Lm1	2.32	1.63	1.26	3.00	1.60
P1585.947	*M. strophensis*	CC	Lm1	2.24	1.78	1.42		
P1585.950	*M. strophensis*	CC	Lm1	x	1.89	x		
P1585.953	*M. strophensis*	CC	Lm1	2.21	1.45	>.92		
Mean		**CC**	**m1**		**1.69**			
SD		**CC**	**m1**		**0.19**			
P2113.775	*M. strophensis*	H	Lm1	2.16	1.58	1.11	3.10	1.70
P2113.774	*M. strophensis*	H	Rm1	2.03	1.52	1.21	2.50	1.30
P2113.780	*M. strophensis*	H	Rm1	1.74	1.53	1.07		
P2113.728	*M. strophensis*	H	Lm1	2.29	1.68	1.21	3.20	1.80
Mean		**H**	**m1**	**2.06**	**1.58**	**1.15**		
SD		**H**	**m1**	**0.24**	**0.07**	**0.07**		
P1585.948	*M. strophensis*	CC	Lm2	2.30	1.70	1.10		
P1585.949	*M. strophensis*	CC	Lm2	2.18	1.87	1.21	2.80	1.60
P1585.951	*M. strophensis*	CC	Rm2	2.10	1.80	1.10	2.50	1.50
P2113.736	*M. strophensis*	H	Lm2	2.13	1.53	1.03		
P2113.734	*M. strophensis*	H	Rm2	2.24	1.68	1.18		
P2113.732	*M. strophensis*	H	Rm2	1.97	1.79	1.16	3.00	1.70
P1585.946	*M. strophensis*	CC	Lm1 or 2	x	x	1.29		
P1585.952	*M. strophensis*	CC	Rm1 or 2	2.05	1.58	1.39		
P1585.954	*M. strophensis*	CC	Rm3	2.00	1.61	0.92		
P1585.955	*M. strophensis*	CC	Rm3	2.11	1.55	0.86		
ROM 6374	*M. strophensis*	CC	Lm3	1.76	1.37	0.84	1.97	1.32
P2113.777	*M. strophensis*	*H*	Lm3	1.71	1.55	0.68		
							LAH	**LBH**
P1585.983	cf *M. montrosensis*	CC	LP4?	x	x	x	1.82	x
P1585.941	cf *M. montrosensis*	CC	RM2	>2.15	3.7	2.8	2.42	1.44
P1585.977	*cf M. montrosensis*	CC	RM1 or 2	x	x	x	2.52x	x

5) Lipotyphla Haeckel 1866

Family incertae sedis

Cryptoryctes C. A. Reed, 1954

Type and only species—*Cryptoryctes kayi* C. A. Reed, 1954.

Diagnosis—As in C. A. Reed, 1954. "Humerus flattened anteroposteriorly and broadened lateromedially; head of humerus elongated in the plane of the long axis of the bone, and placed posterolaterally as compared to its more proximomedial position in small cursorial mammals; lesser tuberosity elongated; greater tuberosity small and not specialized to form a joint with the clavicle; teres tubercle produced medially; distal end of pectoral ridge elevated into a distinct process; capitulum bulbous; capitulum and trochlea lateral in position as contrasted with the more central position in small cursorial mammals; lateral epicondyle produced and sculptured; medial epicondyle extended toward the teres tubercle and bearing a large pit distally; supracondyloid foramen present and elongate."

Cryptoryctes kayi C. A Reed, 1954

Fig. 5.7

Type specimen—FM (CNHM) PM1009, isolated humerus from the Pipestone Springs, Montana

Referred specimens—

Calf Creek Locality:

Left humerus: P661.2132; P661.2136; P661.2137; P661.2138; P661.2140; P661.2143;

P661.2144; P661.2145. Right humerus: P661.2129; P661.2130; P661.2131; P661.2133; P661.2134; P661.2135; P661.2139; P661.2141; P661.2142.

Horse Locality:

Left humerus: P2515.5. Right humerus: P2515.6, P2361.80,

Range (geographic and temporal)—Chadronian of Pipestone Springs, Montana; Canyon Ferry, Montana, Medicine Pole, North Dakota; Cypress Hills, Saskatchewan.

Diagnosis—As for genus.

Description—

Partial to nearly complete humeri matching the description of *Cryptoryctes* are known from both the Calf Creek and Horse localities (Fig. 5.7). The humeri are anteroposteriorly flattened, with flared proximal and distal ends creating a shape reminiscent of an asymmetrical X. The most commonly-found portion consists of the "shaft" from just proximal to the teres tubercle to the medial epicondyle. The capitulum and trochlea are preserved more rarely, and only one specimen, P2361.80, from the Horse Locality, preserves part of the head.

The sharp flange hypothesized by C. A. Reed (1954) for the medial part of the medial epicondyle was not observed in any specimen from the Cypress Hills, although slight breakage medial to the fossa is typical. The trochlea is also not well-preserved.

Reed (1954) listed 5 measurements for *Cryptoryctes* humeri; the same measurements were taken from the Calf Creek and Horse Locality humeri wherever possible, but because Reed did not describe the exact orientation for these measurements, their direct comparability is unclear. The present measurements were taken as follows: total length was measured perpendicular to the line of distal breadth, although this total length was not the complete original

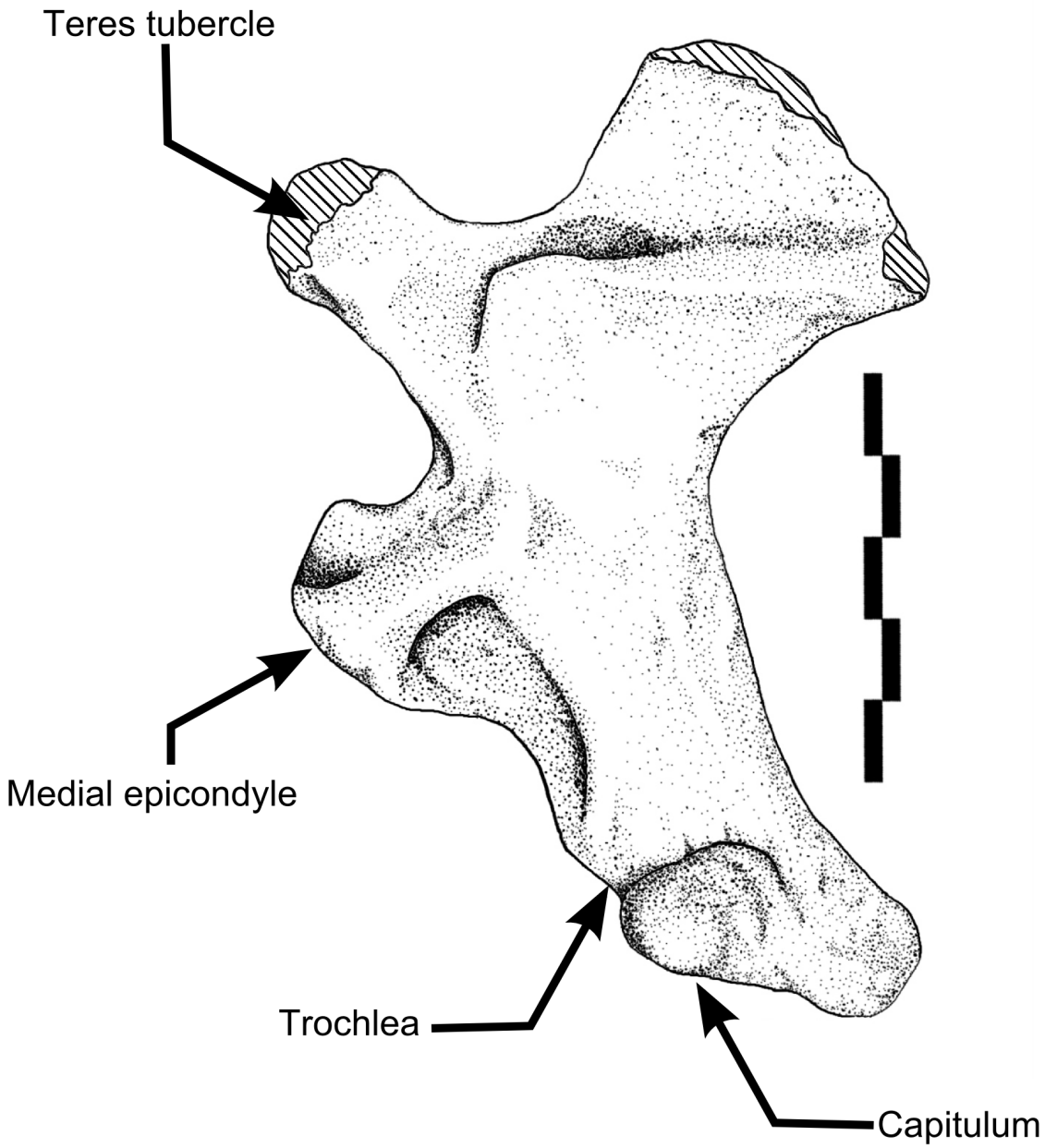


Figure 5.7—Left humerus of *Cryptoryctes*, P2515.005, anterior view.

length in any specimen. Distal breadth was measured in a line between the outer edge of the trochlea and the furthest point on the medial epicondyle. Proximal breadth was not preserved in any of the Cypress Hills specimens. The most consistently available measurements were of the

shaft breadths, measured at the narrowest point on the shaft both proximal and distal to the teres tubercle. The shaft breadth measurements were very similar to those reported by Reed, although falling over a somewhat greater size range, particularly on the smaller end.

Discussion—*Cryptoryctes*, and the related *Arctoryctes*, is a highly-distinctive humerus belonging to a uniquely fossorial animal, with superficial similarities to talpids and chrysochlorids, but distinctly different details; in particular, it lacks the well-developed humeroclavicular joint and transversely tunneled bicipital groove of fossorial talpids (C. A. Reed, 1954). Though C. A. Reed and Turnbull (1965), suggest that a humeroclavicular joint was present in *Arctoryctes*, Barnosky's (1981) description of an articulated *Mesoscalops* skeleton with an *Arctoryctes* humerus refutes this. *Cryptoryctes* has little in common with the chrysochlorid humerus except for the large bicipital groove on the anterior surface (Schlaikjer, 1935).

The dental affinities of the genus have been debated since its first description by C. A. Reed (1954). Reed used head:humerus ratios for various modern fossorial animals to test possible connections with *Apternodus* or the Epoicotheriidae, without striking success; *Apternodus* humeri have since been described (Asher et al., 2002). Russell (1960) used the same technique on an estimated skull-length for *Micropternodus*, achieving a better-fitting ratio than either of Reed's groups; Russell also noted that *Micropternodus* and *Cryptoryctes* co-occurred at the two chief *Micropternodus*-containing faunas known at that time, Canyon Ferry and Pipestone Springs (both in Montana).

Matthew (1928) and Schlaikjer (1935) suggested *Proscalops* as a possibility for the dentition of the related *Arctoryctes*. This suggestion was examined by K. M. Reed (1961) in her review of the Proscalopinae (now generally Proscalopidae), again by comparison of skull-humerus ratios, who found it to be reasonable, though it was noted that no proscalopid was

known at the time from the same aged sediments as *Cryptoryctes*.

Russell (1960) noted similarities between *Micropternodus* rostra and moles (proscalopines not being well known at the time), but recognized that *Micropternodus* could not be a true mole. C. M. Reed and Turnbull (1965) felt that a relationship between *Micropternodus* and proscalopines was more easily supported, as well as making a reasonable circumstantial case for the identity of *Arctoryctes* with *Mesoscalops*. Van Valen (1967) followed K. M. Reed (1960) and C. M. Reed (1965), listing *Cryptoryctes* as a proscalopine, and considered *Arctoryctes* a synonym of *Proscalops*.

Barnosky (1981) described a skeleton of the proscalopid *Mesoscalops*, essentially proving the identity of *Mesoscalops* and *Arctoryctes*. However, he felt that *Cryptoryctes* was too specialized to be the immediate ancestor of *Arctoryctes,* and agreed that *Cryptoryctes* might be linked with *Micropternodus* dentitions, and considered a related family. McKenna and Bell (1997) synonymized *Cryptoryctes* with *Micropternodus,* and *Arctoryctes* with *Proscalops* (not *Mesoscalops)*, but grouped *Micropternodus* with the Soricoidea and proscalopids within the Talpoidea. Unfortunately none of the recent cladistic analyses of the Lipotyphla including fossils (eg. Asher et al., 2002; Asher et al., 2003; Asher et al., 2005), have included proscalopids, nor have they included talpids and micropternodontids together, so the relationships of these three families have never been examined using modern techniques.

The material from the Calf Creek and Horse Localities provides circumstantial evidence for the link between *Micropternodus* and *Cryptoryctes*, another instance of the co-occurrence of these two forms, and neither talpids nor proscalopids have been identified from the Calf Creek and Horse Localities. But until clearly associated cranial and postcranial material is found for any of the groups in question, the true affinities of *Cryptoryctes* will remain speculative.

Table 5.5—Measurements for *Cryptoryctes*; orientations described in text. All measurements are in mm. Mean and standard deviation (SD) are calculated when more than 3 measurements are available from one locality.

Specimen number	Genus	Loc-ality	Humerus side	Total length	Proximal breadth	Distal breadth	Shaft breadth (proximal to teres tubercle)	Shaft breadth (distal to teres tubercle)
P661.2129	*Cryptoryctes*	CC	R			7.6		3.0
P661.2130	*Cryptoryctes*	CC	L				2.7	3.4
P661.2131	*Cryptoryctes*	CC	R					3.3
P661.2132	*Cryptoryctes*	CC	L				3.3	3.3
P661.2133	*Cryptoryctes*	CC	R				3.1	3.3
P661.2134	*Cryptoryctes*	CC	R					2.9
P661.2135	*Cryptoryctes*	CC	R	>9.4		8.1	>3.4	3.6
P661.2136	*Cryptoryctes*	CC	L					3.4
P661.2137	*Cryptoryctes*	CC	L			7.2		3.2
P661.2138	*Cryptoryctes*	CC	L					3.5
P661.2139	*Cryptoryctes*	CC	R			7.6	3.2	3.3
P661.2140	*Cryptoryctes*	CC	L					3.3
P661.2141	*Cryptoryctes*	CC	R					3.7
P661.2142	*Cryptoryctes*	CC	R			7.8		>3.3
P661.2143	*Cryptoryctes*	CC	L					4.0
P661.2144	*Cryptoryctes*	CC	L					3.5
P661.2145	*Cryptoryctes*	CC	L				3.0	3.0
Mean:		**CC**				**7.7**	**3.1**	**3.4**
SD:		**CC**				**0.3**	**0.2**	**0.3**
P2515.005	*Cryptoryctes*	H	L	>11.8	>4.5	9.3	3.3	3.4
P2515.006	*Cryptoryctes*	H	R					3.2
P2361.80	*Cryptoryctes*	H	R				3.5	

6) Lipotyphla Haeckel 1866

Oligoryctidae Asher et al. 2002

Oligoryctes Hough 1956

Type species—*Oligoryctes cameronensis* Hough 1956

Referred species—*Oligoryctes altitalonidus* (Clark, 1937), Tabernacle Butte taxon (as discussed by Asher et al., 2002)

Diagnosis—as in Asher, 2002. *"Oligoryctes* is a shrew-sized animal with zalamdodont molars, lacking metacones and with reduced talonid basins. The m3 talonid cusp is slightly taller than the m3 paraconid. The upper molars have distinct protocones and anterior cingula and the posterior two lower incisors are tricuspid. The medial aspect of the coronoid process is deep or pocketed. *Oligoryctes* has a relatively unspecialized posterior braincase without the elaborate lateral extensions of the squamosal, petromastoid, and occipital that form the lambdoid plates in *Apternodus.* Instead, *Oligoryctes* has a laterally rounded squamosal and petromastoid. It shows a prominent entoglenoid process for posterior support of the jaw joint, medial to the postglenoid foramen and anterior to the promontory of the middle ear. The basicranium shows an enlarged foramen ovale and lacks an alisphenoid canal. The squamosal extends posteriorly along the bentrolateral margin of the braincase, lateral to the large piriform fenstra. The anterior exit of the sinus canal and ethmoid foramen are located well anterior to the sphenorbital fissure and are not incorporated into its superior margin. As in *Apternodus,* the lacrimal foramen is large and laterally oriented."

Discussion—The original diagnosis of Hough (1956) focussed on the cranial morphology of *Oligoryctes*, saying of the dentition only that it was "similar to *Apternodus.*" The diagnosis of

Asher et al. (2002) contains somewhat more dental information. In addition, due to the unusually frequent preservation (or identification) of *Oligoryctes* mandibles at the Calf Creek and Horse Localities, the distinctive morphology of the mandible and coronoid pocket are also useful for the identification of this species.

Asher et al. (2002) classify *Oligoryctes* as incertae sedis above the level of the family; however, their cladistic analysis places *Oligoryctes* close to the Soricidae, and if a monophyletic Lipotyphla does in fact exist it seems highly likely that the Oligoryctidae would fall within it; therefore, for simplicity and in the absence of a strong contrary argument, the Oligoryctidae are here classified within the Lipotyphla.

***Oligoryctes altitalonidus* (Clark, 1937)**

Plate V-B to F

Type specimen—YPM PU13774, left dentary with p4–m3; original lost but casts remain. Microfauna locality, upper Chadron Fm., Big Corral Draw, South Dakota.

Referred specimens—

Calf Creek Locality:

Lowers: P661.489, mandible with condyle, coronoid, root sockets Lm2–3, broken Lm1); P661.492, mandible with coronoid, mandibular condyle, gonial process and roots of Lm3; P1585.932, mandible fragment with Rp3; P661.483, mandible fragment with Lp3; P1585.931, mandible fragment with Lp3; P1585.934, mandible fragment with Rp3–4; P1585.933, mandible fragment with partial Lp3–4; P661.484, mandible fragment with fragments of Lp4, partial coronoid pocket; P661.485, mandible fragment with Lp4, Lm1; P661.487, mandible fragment

with Rp4, Rm1–2; P661.486, mandible fragment with Lp4–Lm1; P1585.935, mandible fragment with partial Rp4, partial Rm1. P661.488, mandible fragment with Lm1, root-sockets of p4, m2–3. P661.490, mandible fragment with Rm2; P1585.938, mandible fragment with Rm2; P1585.936, mandible fragment with Rm1 or 2; P1585.939, mandible fragment with broken Lm; P661.491, mandible fragment with talonid of Lm3.

Horse Locality:

Uppers: P2113.770, RP4 or RM1; P2113.778, RP4 or RM1.

Lowers: P2113.716, mandible fragment with Lp4, Lm1–3, all broken; P2113.718, mandible fragment with Rm1–3; P2187.274, mandible fragment with Lm1–3; P2113.717, mandible fragment with Lm2–3; P2113.714, mandible fragment with Lm2–3; P2482.012, edentulous mandible with root sockets for Rm1-3; P2187.290, Rm1 or 2; P2113.715, Rm?; P2113.886, Rm?; P2113.782, Lm3.

Range (geographic and temporal)—Uintan through Orellan of Wyoming, Montana, South and North Dakota, and Chadronian of Cypress Hills, Saskatchewan. Geographic distribution probably also includes California (Walsh, 1996).

Diagnosis—based on Asher, 2002. Smaller than *O. cameronensis*, larger than Tabernacle Butte taxon. Dental formula 3.1.3.3/3.1.4.3, p1 present, unlike *O. cameronensis.* p3 shows a buccal cingulid. Lower molars do not decrease significantly in width from m1 to m3. Coronoid process is pocketed medially, and bowed (convex) laterally.

Description—

Uppers: two upper molars of *Oligoryctes* have been recovered from the Horse Locality, whereas none at all have been recovered from the Calf Creek. The uppers (Plate V-B, C), have the typical morphology of *Oligoryctes,* being zalamdodont with high paracone, low protocone

and a well-developed preprotocrista (Plate V-B) joining the protocone with the parastylule, while the postprotocrista is much smaller and extends up the posterior surface of the tooth, nearly, but not quite, reaching the mesostyle. They are identified as P4 or M1 due to the buccally prominent metastylar lobe on both specimens; M2 has subequal parastylar and metastylar lobes and the metastylar lobe of the M3 is reduced and shifted lingually. Both teeth are in the size-range of *O. altitalonidus*, smaller, particularly transversely, than those of *O. cameronensis*.

Mandible: *Oligoryctes* is unique among the fossils recovered from the Calf Creek Locality microsite and the Horse Locality in that the majority of the lower molars were recovered in jaw fragments. These jaws show clearly the medially-pocketed coronoid process characteristic of the genus (Plate V-F). The coronoid process is tall, triangular, and angled slightly backwards; the wall of the pocket is very thin, appearing translucent. The lingual surface of the mandible forms a ridge along the bottom of the pocket and the mandibular foramen emerges below the posterior end of this ridge. The mandibular condyle is transverely elongate and angles somewhat medially. A narrow process is also present on the gonial angle of the mandible, exquisitely preserved in P661.492. Externally, the mental foramen emerges below the p2.

p3: the p3 is premolariform, with a single high, pointed cusp, a low anterior cuspule, and a slightly higher posterior cusp similar to the talonids of the molars.

p4-m3: The p4 is molariform, essentially indistinguishable from m1, though smaller. m1 is the highest-crowned of the cheek teeth; crown height reduces towards the m3 (Plate V-D, E). In all molariform teeth, the protoconid is the highest cusp, but it is not as strikingly high relative to other trigonid cusps as in *O. cameronensis*. The metaconid is second highest. In p4, m1, and m2 the paraconid is the third highest cusp, and the single talonid cusp is set low on the posterior face of the trigonid. A slight buccal cingulum is present on some but not all molars. The m3 has a

longer, higher talonid, about half the length of the tooth, though still consisting of a single cusp connected to the trigonid by a crest; there is no talonid basin. The talonid cusp on the m3 is taller than on m1 or 2, rising as high or higher than the paraconid. The molars all have similar widths, the m3 being the narrowest by a very small amount, unlike the molars of *O. cameronensis,* which narrow significantly towards the m3.

Discussion—The features of the Calf Creek and Horse Locality *Oligoryctes* all appear compatible with *Oligoryctes altitalonidus*. The coronoid process of the mandible is deeply pocketed as in *O. altitalonidus* and *O. cameronensis* but unlike the Tabernacle Butte taxon (Asher, 2002). The dentition is smaller than in *O. cameronensis,* and the size of the lower molars does not decrease significantly towards m3, also indicative of *O. altitalonidus*.

The most unusual feature of the Calf Creek and Horse Locality *Oligoryctes* is not the teeth themselves, but rather their preservation. In particular, many of the Horse Locality and all of the Calf Creek Locality specimens are preserved in jaw fragments. This is in stark contrast to the preservation typical of both microsites, where finding even a single tooth embedded in a mandible fragment is very unusual. It seems likely that the small size of the individual teeth (close to 1mm square) prejudices against the recovery of isolated teeth, especially from the Calf Creek Locality, which was excavated in the 1960s and did not use 1mm-mesh screens. However, isolated teeth are also uncommon at the Horse, and uppers (all isolated) are found less commonly than lowers. Similarly unusual preservation of mandibular fragments was also noted for *O. cameronensis* from the Raben Ranch Local Fauna of Nebraska (Ostrander, 1987) and possibly from the Medicine Pole Fauna of North Dakota (Kihm, personal communication, 2007). The reasons behind this bias are unclear. The small size of the teeth explains the rarity of the isolated finds but not the abundance of the tooth-containing mandibles. Edentulous mandibles of other

mammals are also found at the Calf Creek and Horse Localities, but the *Oligoryctes* mandibles typically contain at least some of the dentition, though often damaged. It is possible that the roots of the *Oligoryctes* cheekteeth are particularly robust or well-anchored in the jaw, though the very loose state observed for some of the teeth found in jaws from the Horse Locality prior to consolidation makes this uncertain. Alternatively, *Oligoryctes* may have lived at or close to the environment of deposition, and thus underwent less transport wear and breakage before deposition.

Table 5.6—Measurements of *Oligoryctes altitalonidus*. All measurements are in mm. Mean and standard deviation (SD) are calculated where more than 3 measurements are available from one locality. Mand frag w: mandible fragment with.

Specimen Number	Locality	Element	Description	AP length	Ant width
P2113.770	H	RP4 or RM1	Broken protocone	1.18	X
P2113.778	H	RP4 or RM1		1.21	0.95
P661.483	CC	Lp3	L mand frag w Lp3	1.11	0.58
P1585.931	CC	Lp3	L mand frag w Lp3	1.24	0.66
P1585.932	CC	Rp3	R mand frag w Rm1 or Rm2	1.32	0.63
P1585.934	CC	Rp3	R mand frag w Rp3, Rp4	1.18	0.55
Mean	**CC**	**p3**		**1.21**	**0.61**
SD	**CC**	**p3**		**0.09**	**0.05**
P661.485	CC	Lp4	L mand frag w Lp4, Lm1	1.39	0.84
P661.486	CC	Rp4	R mand. frag w Rp4, Rm1	1.37	0.84
P661.487	CC	Rp4	R mand frag w Rp4, Rm1, Rm2	1.24	0.84
P1585.934	CC	Rp4	R mand frag w Rp3, Rp4	0.92	0.74
Mean	**CC**	**p4**		**1.23**	**0.82**
SD	**CC**	**p4**		**0.22**	**0.05**
P661.485	CC	Lm1	L mand frag w Lp4, Lm1	1.32	1.08
P661.486	CC	Rm1	R mand frag w Rp4, Rm1	1.18	1.00
P661.487	CC	Rm1	R mand frag w Rp4, Rm1, Rm2	1.26	1.05
P661.488	CC	Lm1	L mand frag w Lm1	1.24	1.00
P1585.935	CC	Rm1	R mand frag w partial Rm1-2	x	0.87
Mean	**CC**	**m1**		**1.25**	**1.00**
SD	**CC**	**m1**		**0.06**	**0.08**
P2113.718	H	Rm1	R mand frag w Rm1-3	1.08	0.92
P2187.274	H	Lm1	L mand frag w Lm1-3	1.05	0.86
P661.487	CC	Rm2	R mand frag w Rp4, Rm1, Rm2	1.18	0.97
P661.490	CC	Rm2	R mand frag w Rm2	1.26	1.08
P1585.935	CC	Rm2	R mand frag w partial Rm1-2	x	0.92
P1585.938	CC	Rm2	R mand frag w Rm2	1.08	0.95
Mean	**CC**	**m2**		**1.17**	**0.98**
SD	**CC**	**m2**		**0.09**	**0.07**
P2113.717	H	Lm2	L mand frag w Lm2-3	0.97	0.84
P2113.718	H	Rm2	R mand frag w Rm1-3	0.95	0.92
P2187.274	H	Lm2	L mand frag w Lm1-3	1.11	0.86
P2187.274	H	Lm3	L mand frag w Lm1-3	1.32	0.82
P2113.782	H	Lm3		1.26	0.53
P2113.718	H	Rm3	R mand frag w Rm1-3	1.29	0.74
P2113.717	H	Lm3	L mand frag w Lm2-3	1.18	0.79
Mean	**H**	**m3**		**1.26**	**.72**
SD	**H**	**m3**		**.06**	**.13**
P1585.936	CC	Rm1 or 2	R mand frag w Rm1 or Rm2	0.97	0.97
P2187.290	H	Rm1 or m2		1.08	0.95
P2113.715	H	Rm	Broken talonid	x	0.95
P1585.939	CC	Lm	L mand frag w broken tooth		0.92

iii.

Apatotheria Scott and Jepsen, 1936

Apatemyidae Matthew, 1909

***Sinclairella* Jepsen, 1934**

Type species—*Sinclairella dakotensis* Jepsen, 1934.

Diagnosis—(dentition only, based on the descriptions of Scott and Jepsen, 1936) Teeth brachydont, with low, bulbous cusps; I1 greatly enlarged; premolars nonmolariform. Upper molars quadritubercular, with large hypocone; M2 rectangular in shape while M1 and M3 trapezoid. No conules; buccal shelf present on uppers with or without small cuspules, better developed on M2 than M1. Continuous cutting crest joins small parastyle, paracone and metacone. Lower i1 enlarged, with root extending below molars, but not completely open-rooted. On m1, protoconid and metaconid subequal, paraconid reduced. Ridge down posterobuccal side of protoconid. Crest extends from anterior surface of protoconid, turns lingually, and joins paraconid, forming a transversely-oriented crest on the anterior of the trigonid and giving trigonid square shape; trigonid square narrow in m1, wide in m2 and m3. Talonid basined, with hypoconid distinct but entoconid and hypoconulid reduced to bumps on basin rim. Talonid of m3 greatly expanded posteriorly by a massive hypoconulid.

***Sinclairella dakotensis* Jepsen, 1934**

Plate VI

Type specimen—PU 13585, crushed skull and jaws, Upper Chadron Fm., Big Corral Draw,

South Dakota.

Referred specimens—

Calf Creek:

P661.496, LM2; P661.498, Ri1; 1585.981, Lm1; P661.497, Rm3; P661.2123, Lm3.

ROM (various localities):

ROM 23256, Lm2, "Russell's Hill," but very close to CC; ROM 44357, Lm3, "Calf Creek ±½ mile NE of camp".

Range (geographic and temporal)—Chadronian of Peanut Peak, South Dakota; Raben Ranch, Nebraska; Flagstaff Rim, Wyoming; Medicine Pole, North Dakota; Cypress Hills, Saskatchewan; Orellan of Cedar Creek, Colorado; Whitneyan of Harris Ranch, South Dakota.

Diagnosis—as for genus.

Description—

M2: A waterworn M2 (Plate VI-A) has the basic, quadritubercular shape of a *S. dakotensis* M2, with low, bulbous cusps and a large hypocone forming a distinct postero-lingual lobe. Weak crests join the three main cusps of the trigon, and another joins the protocone to the hypocone. There are no cuspules or well-developed styles visible. The buccal shelf is abraded. The parastyle is a point projecting anterior to the paracone, but may originally have been more extensive. The posterior margin is concave, with a more prominent indent between metacone and hypocone than is illustrated for the type material (Jepsen, 1934). The measurements of this tooth appear rather small for the genus, but are not outside the ranges reported by Ostrander (1987) for the Raben Ranch fauna; the abrasion of the tooth, particularly the parastyle and buccal shelves, has probably artificially reduced the dimensions of the tooth as well.

Lowers:

i1: A lower incisor is identified based on the size, curved, procumbent shape, and distribution of enamel, which is restricted to the convex, inferior and lateral surface of the procumbent tooth; a distinct groove is present on the upper surface of the incisor that is not clearly illustrated in Jepsen's figures (1934:Fig. 3); its depth varies along the length of the tooth, being deepest on the interior of the curve and shallowing towards the tip and the base of the crown.

m1: the m1 (Plate VI-B) is smaller than typical for the species (AP=3.0 mm, typical AP=3.5 mm), but larger than the smallest m1 identified by Ostrander (1987:AP=2.65 mm). Protoconid and metaconid are subequal, with the protoconid being more anteriorly placed. The paraconid is reduced to a low shelf on the anterior of the trigonid. The talonid is wider than the trigonid, and has the form of a broad trapezoidal basin. The large hypoconid is the only distinct cusp on the basin wall; the posterolingual corner of the basin is rounded and flared.

m2: an m2 (Plate VI-C) is known from the ROM collections, derived not from the Calf Creek locality itself but from a nearby site known as "Russell's Hill" worked by the ROM in the 1960s. This m2 is more typical of the size of *Sinclairella dakotensis* than the m1, and illustrates particularly well the anterior crest of the protoconid, which extends anteriorly for a short distance before making a sharp bend lingually to join the paraconid, which is low but better developed than in the m1. A groove separates the metaconid from the paraconid. The talonid is similar to that of the m1.

Three m3s are known, all illustrating the typical morphology of *Sinclairella*, particularly the greatly elongated talonid (Plate VI-D). The trigonid is similar to m2, with a rhombic shape that tilts lingually to the rear. The talonid is an enclosed, elongate basin with bulges along the margin marking the positions of hypoconid and entoconid, and a large and greatly expanded

hypoconulid forming the bulk of the elongation relative to m2.

Discussion—Considering the general rarity of *Sinclairella dakotensis,* a surprising portion of the toothrow is represented at the Calf Creek (with one addition from a neighbouring area). While the upper shows some possibly unusual features, chiefly the small talon and the concave posterior margin, the lower molars fit very well with the described morphologies of *S. dakotensis,* and even the small m1 falls within size-ranges previously reported for the species. Given how little is understood of intraspecific morphological diversity for apatemyids (Clemens, 1964; Ostrander, 1987) and how few specimens are known, it is preferable at this time to refer the Calf Creek *Sinclairella* to the existing species.

Currently, no specimens of *Sinclairella* have been recognized from the Horse Locality. Prothero and Emry (1996, 2004) state that *Sinclairella* first appears in the Late Early Chadronian (except for possible earlier appearance in the Cypress Hills) and disappears before the end of the middle Chadronian; this limited age-range appears to reflect the distribution of *Sinclairella* at Flagstaff Rim, Wyoming, and could support a later date, either later in the Middle Chadronian or in the early late Chadronian, for the Horse Locality. However, the type specimen of *Sinclairella dakotensis* itself originates from the Peanut Peak member of the Chadron Formation in South Dakota, which Prothero and Emry (2004) correlate with the late Chadronian, and Clemens (1964) described two specimens of Orellan age from northeastern Colorado, so clearly this restricted time-range is not broadly applicable. Specimen occurrence may, however, reflect geographic range: Sinclairella appears to occur frequently in the more eastern Chadronian faunas from Nebraska and the Dakotas, intermittently in the central faunas of Wyoming and Saskatchewan, and is completely absent from the Pipestone Springs and other localities in western Montana.

Apatemys Marsh 1872

Type species: *Apatemys bellulus* Marsh 1872

Referred species:

Apatemys bellus Marsh 1872

Apatemys chardini (Jepsen 1930)

Apatemys downsi Gazin 1958

Apatemys hendryi Robinson 1966

Apatemys mutiniacus Russell et al. 1979

Apatemys rodens Troxell 1923

Apatemys sigogneaui Russell et al. 1979

Apatemys teilhardi Russell et al. 1979

Apatemys uintensis (Matthew 1921)

Range (geographic and temporal)—Late Paleocene to late Eocene of North America; Early Eocene of Europe.

Diagnosis—(Based on descriptions of West and Atkins, 1970). P3 large, single-rooted, with high, posteriorly curved main cusp and anterior and posterior cuspules; leaflike lateral appearance. P4 3-rooted and semimolariform, unlike P4 of *Stehlinella* or *Sinclairella*; large buccal paracone and well-developed parastyle; posterior crest extends from paracone to weak metastyle; moderately large protocone. M1 three-rooted, much larger than P4; large parastyle in front of slight ectoflexus; ectoflexus deeper than in *Sinclairella*; distinct para- and meta-cristae; paracone slightly higher than metacone; protocone large and slightly lower than buccal cusps;

hypocone low, placed far posterolinguad; slight crests extend from protocone to paracone and metacone, creating a small, shallow internal basin. M2 has large, prominent parastyle and metastyle, separated by wide ectoflexus; paracone and metacone as in M1; prominent protocone; hypocone forming small bulge on posterolingual flank of protocone base; no intermediate conules; low crest on anterior side of central basin from protocone to paracone-preparacrista junction elevates anterior half of central basin. M3 smaller than M1 or 2; parastyle large and extending anterobuccally; metacone and metastyle reduced; hypocone absent; weak crest along anterior margin of central basin.

Discussion—There are no published modern diagnoses of *Apatemys.* McKenna (1963) states: "It is not practical to give a diagnosis of this... apatemyid at this time," and the situation does not appear to have been remedied since. The above diagnosis concerns only the upper molars, since no lowers from the Cypress Hills are referred to *Apatemys,* and is based closely on the descriptions of Bridgerian *Apatemys* uppers by West and Atkins (1970); it appears broadly consistent with the *Apatemys* uppers figured by McKenna (1963) and the European specimens described and figured by Russell et al. (1979). However, *Apatemys* species are generally based on isolated lower dentitions, and the specific affiliations of the upper molars is often uncertain.

Apatemys sp.

Fig. 5.8

Referred specimen—

Calf Creek: P2374.006, LM2

Description—A single, unworn M2 is referred to *Apatemys.* Its overall shape is rectangular. A low paraconule is present anterobuccal to the protocone. A distinct sectorial ridge runs

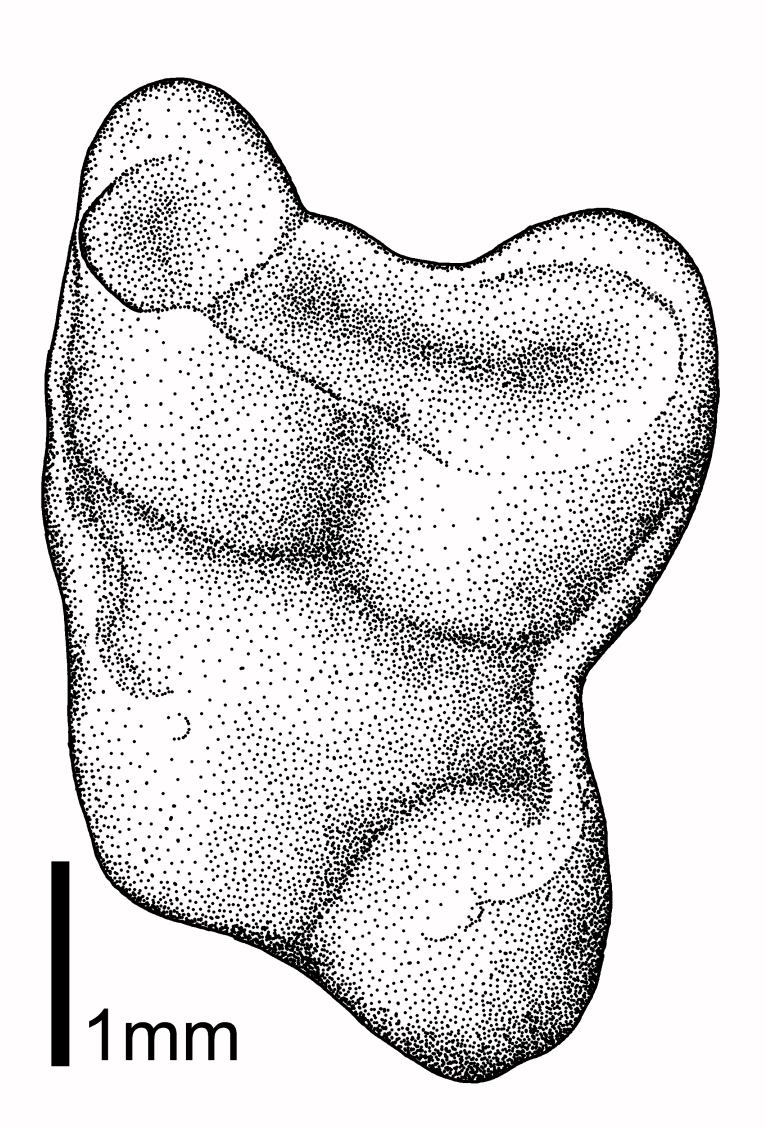


Figure 5.8—*Apatemys* sp. P2374.006, LM2, occlusal view.

anteroposteriorly along the paracone and metacone, joining them and curving buccally anterior to the paracone to the parastylar lobe and posterior to the metacone into the metastylar lobe. The buccal shelf is very well developed, with prominent lobes extending buccally in the region of the parastyle and metastyle and a deep ectoflexus between them. The middle of the shelf is convex, with a slight protrusion where the buccal face of the paracone touches it. The shelf is rimmed by a low ridge, creating a shallow basin, but styles are not clearly present. The large hypocone, which forms a distinct lobe on the posterolingual margin of the tooth, is lower than the protocone and is displaced lingually relative to the protocone. The talon is small, and less basined than in illustrated specimens.

Discussion—P2374.006 is strikingly similar to AMNH 56046, an *Apatemys* M2 described by West and Atkins (1970) from the Bridgerian of Wyoming. In particular the stylar shelves of the two teeth are near identical. The metastylar lobe is wide, rounded and basined, narrowing posteriorly. There is a small swelling lingual to the paracone, directly posterior of the narrow,

sharply-jutting parastylar lobe. The chief difference between the two teeth is in the form of the hypocone and talon; in AMNH 56046, the hypocone is fairly small, with a buccal crest appressed close to the posterior margin of the tooth. In P2374.006, the hypocone is larger and fully conical, occupying a distinct lobe jutting out from the posterolingual margin of the tooth, and its buccal crest is less distinct. P2374.006 also lacks the metaconule-like cusp of AMNH 56046 and has a small protoconule on the preprotocrista.

Upper molars of *Sinclairella* lack the expansive stylar lobes found on P2374.006 and have a more quadrate shape, whereas P2374.006 is more triangular. Unfortunately most *Apatemys* species are based on the lowers alone and diagnoses which include uppers are nonexistant. Further comparison with a wider range of apatemyid uppers would be beneficial, particularly since *Apatemys* is otherwise unknown from the Chadronian. Its presence in the Calf Creek Local Fauna could support the earlier dates for the site favoured by Storer (1996), but may equally represent a local survival of a very rare taxon.

Storer (1996) listed *Apatemys* sp. as present at the Calf Creek Locality; however, when RSM and ROM collections from the site were examined no specimens previously identified as belonging to *Apatemys* were found. The current specimen was referred to Apatemyidae, gen. et sp. indet; it was probably the basis for Storer's reference.

Table 5.7—Measurements for *Sinclairella dakotensis* and *Apatemys sp.* All measurements are in mm.

Specimen Number	Species	Locality	Element	AP length	Ant width	Post width	LAH	LBH
P661.496	*S. dakotensis*	CC	LM2	2.6	2.7	3.0	2.0	2.3
							LOT	
P661.498	*S. dakotensis*	CC	Ri	>10.2	n/a	1.9	n/a	n/a
P1585.981	*S. dakotensis*	CC	Lm1	3.0	1.8	2.1	1.7	n/a
ROM 23256	*S. dakotensis*	Russell's Hill	Lm2	3.8	2.6	2.5	2.0	n/a
P661.2123	*S. dakotensis*	CC	Lm3	5.3	2.2	1.4	2.0	n/a
P661.497	*S. dakotensis*	CC	Rm3	4.9	2.2	1.4	x	n/a
ROM 44357	*S. dakotensis*	"Calf Creek"	Lm3	5.2	2.5	2.4	2.0	n/a
P2374.006	*Apatemys* sp.	CC	LM2	3.3	4.0	4.4	2.5	2.6

iv.

Leptictida McKenna 1975

Leptictidae Gill, 1872

Leptictinae Gill, 1872

***Leptictis* Leidy, 1968**

Type species—*Leptictis haydeni,* Leidy1868

Referred species—

Leptictis dakotensis (Leidy) 1968

Leptictis bullatus (Matthew) 1899

Leptictis acutidens (Douglass) 1903

Leptictis thomsoni (Matthew) 1903

Leptictis douglassi Novacek, 1976

Leptictis wilsoni Novacek, 1976

Range (geographic and temporal)—Chadronian to Arikareean of North America.

Diagnosis—(based on diagnosis provided for *Ictops,* Scott and Jepsen, 1936)

Upper incisors with single roots, chisel-like crowns without cingulum or basal cusps. Upper canine relatively large, especially antero-posteriorly. Upper premolars increase in size from P1-P3. P1 minute, compressed-conical crown with two roots. P2 similar to P1 but much larger. P3 with three external cusps, central cusp largest, and prominent internal cusp. P4 molariform. Upper molars: paracone and metacone conical, protocone crescentic. “Arms” of protocone display conules when unworn. Prominent posterior cingulum and small hypocone create rectangular molar shape; much wider than long. Small anterior cingulum may also be

present. M3 reduced and triangular, lacking hypocone, posterior cingulum and metacone reduced or absent.

Lower incisors small and styliform, roots large and cylindrical, minute conical crowns. Lower canine small and incisiform, slightly larger than and offset from incisors. Lower premolars: similar to uppers except for p4. p1 single-rooted. p2 larger with incipient posterior cingulum. p3 largest with anterior and posterior basal cusps, no interior cusp. p4 partially molariform with a posterior heel. Lower molars: molars diminish in size posteriorly. Trigonids have two main cusps (protoconid and metaconid). Paraconid reduced or absent, centrally placed when present. Talonid of m3 laterally compressed.

Discussion—Several publications (Emry, 1992; Prothero and Emry, 1996; Prothero and Emry, 2004) refer to a Chadronian leptictid called "*Frictops emryi*", a nomen nudum (scientific name with no published meaning, and therefore not valid under the International Code of Zoological Nomenclature) apparently originating from the unpublished PhD work of Dr. Michael J. Novacek; it is probably a subset of *Leptictis acutidens*, but has never been formally published (Meehan, pers. comm. 2007). It seems likely that some or all of the leptictids present at the Calf Creek and Horse Localities represent species which would be referred to "*Frictops",* but since a description or diagnosis is not available this possibility cannot be assessed. AMNH online records currently list the holotypes of *L. acutidens* and *L. thompsoni* under the genus "*Fricktops"* (spelling intentional), and it seems likely that *L. wilsoni* might also fall in this genus, should it be published.

Leptictis acutidens **(Douglas 1903)**

Plate VII

Type specimen—AMNH 9604, portions of skull, mandible, and partial skeleton of a young

individual. Pipestone Springs Local Fauna, middle Chadronian, Montana.

Referred specimens—

Calf Creek Locality:

Uppers: P661.2125, LDP3; P1585.1042 RDP3; ROM 44356, RP3; P1585.982, RP3; P661.465, RP3; ROM 23245, LM1 or 2; ROM 6243, LM1 or 2; P661.466, RM1 or 2; P661.2126, RM1 or 2; P1585.908, LM3; P1585.909, LM3; P1585.910, RM3; P1585.911, RM3; P661.468, LM3; P1585.906, LM1 or 2 (lingual margin only).

Lowers: ROM 6244, Lm1 or 2; P1585.914, Lm1 or2; P661.476, Lm1 or 2; P661.472, Lm1 or 2; P1585.919, Rm1 or 2; P661.470, Rm1 or 2; P661.469, Lm1 or 2; P661.471, Lm1 or 2; P661.475, Rm1 or 2; P661.478, Rm1 or 2; P1585.915, Rm1 or 2; P1585.920, Rm1 or 2 talonid; P1585.913, Lm1 or 2, damaged talonid; P1585.916, Lm1 or 2, talonid; P1585.921, Lm1 or 2, talonid; P1585.912, Lm1 or 2, trigonid; P661.473, Rm3; P661.474, Rm3 talonid only.

Horse Locality:

Uppers: P2187.245, LP4; P2430.133, LP4, broken, lingual margin only; P2483.009, LM1 or 2 P2113.744, RM1 or 2; P2113.738, RM1 or 2; P2431.006, LM1 or 2; P2113.739, LM1 or 2, broken posterobuccal margin; P2113.746, RM1 or 2; P2476.011, RM1 or 2, broken, buccal margin only; P2113.740, LM1 or 2, buccal margin only; P2187.279, RM1 or 2, buccal margin only; P2113.741, LM1 or 2, buccal margin only; P2113.737, LM3; P2113.745, LM3.

Lowers: P2113.003, Rp4; P2482.011, Rp4, trigonid only; P2187.278, Rm1 or 2; P2475.018, Rm1 or 2; P2113.742, Rm1 or 2; P2430.132**,** Lm1 or 2, trigonid damaged; P2113.743, Rm1 or 2, talonid only.

Range (geographic and temporal)—middle Chadronian of western Montana, Wyoming, Nebraska, North Dakota, and Saskatchewan.

Diagnosis—based on Novacek, 1976. Smaller than *Leptictis dakotensis, L. haydeni, L. douglassi,* and *L. montanus.* Similar in size to *L. wilsoni, L. thomsoni.* Cusps less sharp and piercing than *L. thomsoni,* possesses anterior cingulum, unlike *L. thomsoni.* Anterior cingulum positioned roughly midway along anterior margin of the tooth, not at lingual margin as in *L. wilsoni.* More constricted through the midline of the tooth than *L. wilsoni;* longer (less transversely compressed) than *L. thomsoni*.

Description—

Uppers:

DP3 and P3: P3 consists of a high central cusp (paracone) flanked by a lower metacone posterad and a very low parastyle anterad. These three cusps are arranged in a line. An interior cusp (protocone) is present on the lingual margin, just posterior to the paracone, giving the tooth a "T" shape in occlusal view (Plate VII-B). P661.2125 (Plate VII-A, D) from the Calf Creek appears to represent a DP3. The margins of the protocone angle into the buccal line of cusps, forming a more triangular, rather than "T" shaped, tooth, and the lingual margin of the protocone angles posteriorly. There is a greater separation between the paracone and the metacone, and the metacone is narrower and more bladelike than in the permanent dentition. The anterior parastyle is somewhat longer but narrower than the permanent dentition, as well. A buccal cingulum is present along the posterior half of the tooth. DP3 is also much lower-crowned than the P3s (Plate VII-D, E). P661.2125 compares well with the DP3 in CM9580, a partial maxilla referred to *L. acutidens* from the Pipestone Springs Locality of Montana, which also has the triangular shape, long, narrow parastyle, low crown, and bladelike metacone.

P4: P4 is molariform, but longer and narrower than the molars (Plate VII-C). The parastyle is large and cuspate. The paracone is higher than the metacone. A postmetacrista along

the posterior face of the metacone connects to the metastyle. The preprotocrista is higher than the postprotocrista; a protoconule is present on the preprotocrista but becomes flattened with moderate wear. The protocone is narrow and triangular, although the small hypocone adds width to the lingual margin of the tooth. The short anterior cingulum extends along the front of the tooth from the level of the buccal margin of the protocone to the protoconule; it does not reach the lingual margin of the protocone.

M1 and 2: M1 and 2 are relatively wide, short teeth, not easily distinguished in isolated specimens. The trigon is triangular, but a well-developed hypocone and shelf gives the overall tooth a roughly rectangular shape. Parastylar and metastylar lobes are present but variably developed, ranging from small points at the anterior and posterior buccal margins of the tooth, joined by a narrow buccal cingulum (Plate VII-G), to broad, basined lobes extending more buccally from the paracone and metacone (Plate VII-F). Small proto- and metaconules are present on the preprotocrista and postprotocrista respectively, but may be obliterated with wear. The preprotocrista is higher than the postprotocrista. The hypocone is a well-developed cusp with a crest extending buccally along the posterior margin of the talon; a small secondary cusp (hypoconule?) buccal to the hypocone is present on one specimen (P2113.739); a similar cusp is present on reference specimen CM 9580 from the Pipestone Springs Locality of Montana, attributed to *L. acutidens,* and also on one of the specimens referred to *Leptictis wilsoni* (P2113.002, Plate VIII-B). It seems likely that this cuspule is variable in *L. acutidens*. The anterior cingulum is variable in length and width, but is always positioned between the protocone and the protoconule, and does not reach the lingual margin of the tooth. In one case (P2113.739), there is almost no anterior cingulum, only a tiny irregularity in the enamel on the anterior face of the tooth.

M3: M3 (Plate VII-H) is more triangular than the anterior molars, largely because the hypocone is reduced to a narrow posterior shelf. The paracone and parastyle are well-developed. The metacone is reduced but the condition is variable, ranging from a small, well-developed cusp, to a low, posterior-angling projection to only a rounded crest running posteriorly from the base of the paracone to the posterobuccal corner of the tooth and turning to join the postprotocristid. The anterior cingulum is absent.

Lowers:

p4: p4 is molariform and large (Plate VII-K). The trigonid is distinctive relative to the molars in that it has a large, cuspate (but low) paraconid; the paraconid has anterior and posterior crests angling from the posterobuccal side of the cusp across the apex and down the anterolingual margin. The protoconid and metaconid are similar in size, but much higher, the metaconid being the highest. A crest joins the middle of the posterior face of the trigonid to the hypoconid, angling posterobuccally. The hypoconid is the only well-developed cusp of the talonid, and is about the same height as the paraconid. A crest curves from the hypoconid lingually along the posterior margin of the tooth, but though it has some irregularities, there are no clearly-developed cusps, and a gentle swelling in the position of the entoconid. The lingual margin of the talonid is a low notch.

m1 or 2: m1 or 2 is slightly smaller than the p4 (Plate VII-J). The protoconid and metaconid are similar to those in the P4, but the paraconid is reduced, being a small nub set almost centrally at the junction of the protoconid and metaconid. A short crest connects it to the protoconid, while a notch separates it from the metaconid. There is also a low anterior cingulum angling up the anterobuccal margin of the trigonid to the base of the paraconid. The talonid is lower and has three well-developed, subequal cusps curving along the posterior margin of the

tooth, hypoconid, hypoconulid, and entoconid. An oblique crest connects the trigonid and hypoconid as in the P4, while between the entoconid and the trigonid is a deep notch. A tiny cuspule anterior to the entoconid is present on unworn specimens.

m3: The only complete m3 (P661.473, Plate VII-I) has a damaged protoconid; other m3s are known from isolated talonids. The trigonid resembles that of m1 or 2, but is relatively narrow (compressed transversely). The talonid is even more compressed, and the hypoconulid extends distinctly further posterior to the hypoconid and entoconid than in the m1 and 2. Also, the notch between the entoconid and the trigonid is much shallower, being occupied by a very low crest.

Discussion—Most of the Cypress Hills *Leptictis* appears to belong to this species, although its characteristics are quite variable. The measurements for the uppers show significant size variability; however, on examination the smaller teeth were always more worn and abraded, often showing minor breakage of the stylar lobes, so the size differences appear to be largely due to post-mortem factors. It seems possible that some of the lowers, perhaps the more robust ones, may actually belong to *L. wilsoni*; however since no lowers have been described for this species, they cannot be identified.

***Leptictis wilsoni* Novacek 1976**

Plate VIII-A to C

Type specimen—TMM 40209-215, partial skull with upper toothrows, Little Egypt Local Fauna of the Vieja Group, earliest Chadronian, Texas.

Referred specimens—

Calf Creek Locality: P661.2124, RP4

Horse Locality: P2113.002, LM1

Range (geographic and temporal)—earliest Chadronian of the Vieja Group, Texas; middle Chadronian of Saskatchewan.

Diagnosis—from Novacek, 1976. "Skull and dentition significantly smaller than those referred to *Leptictis haydeni, L. dakotensis, L. bullatus,* and *L. douglassi;* zygomatic arch narrow, no dorsoventral swelling of the jugal; paroccipital process or squamosal flange not strongly produced ventrally; shallow antorbital fossa; depression in back of the zygomatic process of squamosal for opening of the subsquamosal foramen very shallow; P3 tricuspid with lingual and anterior spurs; molariform P4 longer but not quite as wide as M1 with hypocone and precingulum; M1-3 with well developed hypocones, precingula, and labial spurs; molar cusps conical but not swollen at their bases or bulbous; M3 not greatly reduced relative to M1-2 with stronger metacone than in most species of *Leptictis;* length P3-M3 14.52 mm."

Novacek (1976) observes the following diagnostic criteria in the discussion of *Leptictis wilsoni*: smaller than all other *Leptictis* species except for *L. acutidens* and *L. thomsoni*. Larger than *L. thomsoni* with as less piercing, less transverse teeth; possesses precingula and hypocones on P4 and M3, unlike *L. thomsoni.* Similar in size to *L. acutidens* but has larger P4 and M3, more transverse upper molars, lingually positioned precingula (anterior cingula), and weaker buccal lobes.

Description—Two teeth, one from each locality, are referred to *Leptictis wilsoni;* they are broader across the midline (buccal to the hypocone) than is typical of *L. acutidens* or *L. thomsoni*, and the anterior cingulum extends to the lingual margin of the tooth.

P4: The P4 (Plate VIII-C) is typical of *Leptictis* P4s in resembling the molars but being somewhat narrower and longer. The anterior cingulum begins at the lingual margin of the protocone, as in *L. wilsoni*, and the tooth is longer through the midline (less transversely

compressed) than P4s of *L. acutidens*, again as in *L. wilsoni* It has a large parastylar cusp and a conical paracone and metacone, the paracone being higher. The buccal shelf is present only as a narrow cingulum. There is a very low postmetacrista running down the posterior face of the metacone to the small metastylar lobe. A very large protoconule is present on the preprotocrista, also similar to the *L. wilsoni* type, but there is no metaconule. There is a relatively small hypocone and posterior cingulum..

M1: The M1 is almost unworn and in excellent condition (Plate VIII-A, B). Only the slightest of wear facets are visible on the protocone and pre- and postprotocristae, both of which show small para- and metaconules. The stylar lobes are well developed but slightly damaged on the anterior and posterior buccal corners, especially the metastylar lobe; there is a slight irregularity in the enamel of the stylar ridge between the protocone and metacone. The hypocone is large and the hypoconal shelf (posterior cingulum) is well-developed, extending buccally to just lingual to the metacone. Buccal to the hypocone is another tiny cusupule (hypoconule) on the posterior rim of of the shelf (Plate VII-B). The anterior cingulum is large and runs from the lingual margin of the protocone to just lingual of the paracone. The most striking feature of the anterior cingulum is that it is ornamented, almost serrated, by a row of tiny cuspules.

Discussion—These two teeth appear to belong to *Leptictis wilsoni*. They are less transversely compressed through the middle of the tooth than *L. acutidens* or *L. thomsoni,* and show the lingually-positioned anterior cingulum.

The hypocone shelves of the *L. wilsoni* type show a slight irregularity in the wear-facets buccal to the hypocone, which could be the remnants of a cuspule like the one present on P2113.002. Similar cuspules, discussed above, are present in some specimens otherwise referable to *L. acutidens;* this may be a variable feature in either or both species. The *L. wilsoni* holotype

also shows some irregularity of enamel on the stylar shelf, which matches closely the pattern on the buccal margin of P2113.002. The distinctive row of cuspules on the anterior cingulum of P2113.002 is not present on the anterior cingula of the type, but the latter cingula are worn, which could have obliterated tiny cuspules; the feature may also be individually variable.

Leptictis wilsoni has previously been known only from the type, from the earliest Chadronian Little Egypt Local Fauna of Texas. Identification of this species from the mid Chadronian of Saskatchewan increases the geographic and temporal range of the species considerably.

***Leptictis thomsoni* (Matthew 1903)**

Plate VIII-D to F

Type specimen—AMNH 9606, maxilla with P4-M3, Pipestone Springs Local Fauna, middle Chadronian, Montana.

Referred specimens—

Calf Creek Locality:

Uppers: P661.467, RM1 or 2; (?)P1595.907, RM1 or 2.

Lowers: (?)P1585.984, Rp4; (?)P1585.917, Lm1 or 2; (?)P1585.918, Lm1 or 2.

Range (geographic and temporal)—middle Chadronian of western Montana, Saskatchewan.

Diagnosis—(based on Novacek, 1976) Smaller, more anteroposteriorly compressed teeth than *L. acutidens*. Cusps more pointed. Metacone distinctly smaller than protocone. Anterior cingulum absent, hypocone reduced or absent on P4 and M3.

Description—

A single M1 or 2 (Plate VIII-D) is similar in width to the *Leptictis acutidens* specimens

but much shorter anteroposteriorly, showing the transverse compression typical of *L. thomsoni*. It lacks an anterior cingulum, and has a very small hypocone and posterior cingulum. The stylar lobes appear to be very small, but the tooth enamel is pitted and etched, making it difficult to assess abrasion or minor breakage.

Several specimens from the Calf Creek Locality that may represent *L. thomsoni*, but show some deviations from the published descriptions, are described next:

P1585.907 (Plate VIII-E): this tooth resembles *Leptictis thomsoni* in general form but shows certain differences, particularly the broad, expanded metastylar lobe. The tooth is very short anteroposteriorly, being transversely compressed like *L. thomsoni*. The paracone and metacone are conical but appressed, in contact for most of their height. There is no anterior cingulum, nor is there a hypocone, again as in *L. thomsoni*. The metacone is slightly smaller than the paracone and more buccally placed, and a postmetacrista curves posterolingually from the metacone to the metastylar lobe, though it is interrupted by a notch posterior to the metacone. The protocone is very narrow, and the worn remnants of protoconule and metaconule touch on the narrow trigon. Buccal to the metaconule the postprotocrista runs down and ends low on the side of the tooth, below the base of the metacone; it does not connect with the metastyle. The preprotocrista ends at the base of the paracone. The anterobuccal corner of the paracone and the parastyle are missing.

Three lower cheekteeth, P1585.984, P1585.917, and P1585.918, are smaller than the majority of the *L. acutidens* specimens, particularly in width; these may represent specimens belonging to *L. thomsoni*. P1585.984 (Plate VII-F) has a damaged paraconid, but still shows that the paraconid was separate from the other cusps of the trigonid, as in a *Leptictis* p4, not small and located high between the protoconid and metaconid as in molars of *Leptictis*. However, the

talonid is fully developed, with three cusps along its posterior margin, unlike the talonid in the p4 of *L. acutidens* (Plate VII-K). This tooth is considerably smaller than the p4 recognized for *L. acutidens*. If it does belong to *L. thomsoni,* then the p4 of *L. thomsoni* is more molariform in the morphology of its talonid than that of *L. acutidens*. The other two specimens resemble the lowers of *L. acutidens* except for their smaller size.

Discussion—The transverse shape and lack of an anterior cingulum in P661.467 are typical of *Leptictis thomsoni.* The pitted enamel may indicate more extensive transport of this tooth, suggesting that *L. thomsoni* was a "rare erratic" in the area of deposition, perhaps inhabiting more distant areas or areas further from water.

A broadly expanded stylar lobe similar to that on P1585.907 is seen in some of the other *Leptictis* specimens from the Calf Creek and Horse Localities (eg. P2483.009, Plate VII-F, referred to *L. acutidens*), though not to the same extent relative to the size of the tooth; this condition appears to be quite variable, however broad stylar lobes have not been observed in published specimens of *L. thomsoni*. The absence of both anterior cingulum and hypocone is noted by Novacek (1976) as being a characteristic of the P4 and M3 of *L. thomsoni,* but the well-developed metacone and metastyle are not typical of an M3 and the tooth seems too wide transversely and compressed anteroposteriorly to be a P4, even of the compressed *L. thomsoni*. The appressed metacone and paracone resemble those in the M1 of *Micropternodus,* but the tooth is much more transversely compressed than *Micropternodus* and notably lacks the well-developed hypocone characteristic of that genus. It is also considerably larger than typical specimens of *Micropternodus*.

The lower molars are referred to *Leptictis thomsoni* largely due to their smaller size, particularly buccolingually.

Table 5.8—Measurements for Leptictis. All measurements are in mm. Mean and standard deviation (SD) are calculated where more than 3 measurements are available from one locality. WTJ signifies width at talonid-trigonid junction.

Specimen Number	*Species*	Locality	Element	AP length	Ant width	Post width	LAH	LBH
P1585.1042	*L. acutidens*	CC	RDP3	3.7	1.2	x	n/a	n/a
P661.2125	*L. acutidens*	CC	LDP3	3.6	1.1	2.3	n/a	n/a
P661.465	*L. acutidens*	CC	RP3	3.5	1.2	2.5	n/a	n/a
P1585.982	*L. acutidens*	CC	RP3	x	x	2.6	n/a	n/a
ROM 44356	*L. acutidens*	CC	RP3	3.3	1.2	2.3	n/a	n/a
P2187.245	*L. acutidens*	H	LP4	2.8	3.5	1.8	1.6	
P2430.133	*L. acutidens*	H	LP4	3.3	2.3	n/a	n/a	n/a
P661.2126	*L. acutidens*	CC	RM1 or 2	2.6	4.1	4.0	2.0	1.8
P661.466	*L. acutidens*	CC	RM1 or 2	2.5	3.8	3.9	1.7	1.5
P661.478	*L. acutidens*	CC	RM1 or 2	3.2	2.3	1.9	1.3	1.8
P1585.903	*L. acutidens*	CC	RM1 or 2	2.8	x	x	1.8	1.6
ROMVP 23245	*L. acutidens*	CC	LM1 or 2	2.9	4.3	4.5	2.1	1.8
ROMVP 6243	*L. acutidens*	CC	LM1 or 2	2.8	4.6	4.7	2.1	1.8
Mean	***L. acutidens***	**CC**	**M1 or 2**	**2.8**	**3.8**	**3.8**	**1.8**	**1.7**
SD	***L. acutidens***	**CC**	**M1 or 2**	**0.2**	**0.9**	**1.1**	**0.3**	**0.1**
P2113.739	*L. acutidens*	H	LM1 or 2	x	x	3.7	1.9	1.7
P2113.740	*L. acutidens*	H	LM1 or 2	x	x	x	2.1	1.7
P2113.741	*L. acutidens*	H	LM1 or 2	x	x	x	2.1	1.8
P2113.744	*L. acutidens*	H	RM1 or 2	2.4	3.5	3.7	1.9	1.6
P2431.006	*L. acutidens*	H	LM1 or 2	3.0	x	x	x	1.6
P2113.746	*L. acutidens*	H	LM1 or 2	2.8	>3.8	3.7	x	1.7
P2476.011	*L. acutidens*	H	RM1 or 2	x	x	x	2.4	2.0
P2483.009	*L. acutidens*	H	LM1 or 2	2.9	4.5	4.7	2.0	1.7
Mean	***L. acutidens***	**H**	**M1 or 2**	**2.8**		**4.0**	**2.1**	**1.7**
SD	***L. acutidens***	**H**	**M1 or 2**	**0.3**		**0.5**	**0.2**	**0.1**
P1585.908 (LL 408)	*L. acutidens*	CC	LM3	1.5	3.0	2.3	1.2	1.1
P1585.909	*L. acutidens*	CC	LM3	2.0	>2.7	>2.1	1.1	1.1
P1585.910	*L. acutidens*	CC	RM3	1.5	2.9	2.1	1.4	1.3
P1585.911	*L. acutidens*	CC	RM3	1.9	3.7	2.8	1.1	1.1
Mean	***L. acutidens***	**CC**	**M3**	**1.7**	**3.2**	**2.4**	**1.2**	**1.2**
SD	***L. acutidens***	**CC**	**M3**	**0.3**	**0.4**	**0.4**	**0.1**	**0.1**
P2113.737	*L. acutidens*	H	LM3	>2	>3.5	3.1	1.0	1.3
P2113.745	*L. acutidens*	H	LM3	2.1	3.5	3.1	1.4	1.4
							LOT	**WTJ**
P2113.003	*L. acutidens*	H	Rp4	4.0	2.3	2.1	1.7	1.3
P2482.011	*L. acutidens*	H	Rp4	3.0	2.2	n/a	n/a	n/a
P661.469	*L. acutidens*	CC	Lm1 or 2	2.9	2.2	2.0	1.6	1.6
P661.470	*L. acutidens*	CC	Rm1 or 2	2.8	2.1	1.8	1.0	1.8
P661.471	*L. acutidens*	CC	Lm1 or 2	3.2	2.0	1.7	1.4	1.5
P661.472	*L. acutidens*	CC	Lm1 or 2	3.0	2.4	2.1	1.5	1.9
P661.476	*L. acutidens*	CC	Lm1 or 2	2.8	2.4	2.0	1.3	1.9
P1585.914	*L. acutidens*	CC	Lm1 or 2	3.1	2.2	1.8	1.5	1.6
P1585.915	*L. acutidens*	CC	Rm1 or 2	2.8	2.5	2.0	1.2	1.8
P1585.919	*L. acutidens*	CC	Rm1 or 2	3.2	2.2	1.9	1.4	1.7
PROM 6244	*L. acutidens*	CC	Lm1 or 2	3.0	2.2	2.0	1.4	1.7
P661.475	*L. acutidens*	CC	Rm1 or 2	2.9	1.9	1.8	1.3	1.5

Mean	***L. acutidens***	**CC**	**m1 or 2**	**3.0**	**2.2**	**1.9**	**1.4**	**1.7**
SD	***L. acutidens***	**CC**	**m1 or 2**	**0.2**	**0.2**	**0.1**	**0.2**	**0.1**
P2113.738	*L. acutidens*	H	Rm1 or 2	x	x	3.8	1.8	1.5
P2113.742	*L. acutidens*	H	Rm1 or 2	3.0	2.1	2.2	1.5	1.3
P2113.743	*L. acutidens*	H	Rm talonid	x	x	1.7	>1.3	0.9
P2187.278	*L. acutidens*	H	Rm1 or 2	3.0	2.2	1.9	1.8	1.2
P2187.279	*L. acutidens*	H	Rm1 or 2	x	x	x	1.9	1.8
P2430.132	*L. acutidens*	H	Lm1 or 2	x	x	1.9	1.8	1.2
P2475.018	*L. acutidens*	H	Rm1 or 2	3.2	2.1	2.0	1.8	1.1
Mean	***L. acutidens***	**H**	**m1 or 2**			**2.3**	**1.8**	**1.3**
SD	***L. acutidens***	**H**	**m1 or 2**			**0.8**	**0.1**	**0.3**
P661.473	*L. acutidens*	CC	Rm3	3.2	1.7	1.4	1.1	1.3
P661.474	*L. acutidens*	CC	Rm3	x	x	1.4	x	x
							LAH	**LBH**
P2113.002	*L. wilsoni*	H	LM1	3.0	4.4	4.5	2.6	1.9
P661.2124	*L. wilsoni*	CC	RP4	3.3	3.7	3.7	1.9	1.8
661.467	*L. thomsoni*	CC	RM1 or 2	2.1	4.1	4.0	1.2	1.5
1585.907	*L. ?thomsoni*	CC	RM1?	>2.0	3.9	>3.0	1.2	1.4
							LAT	**WTJ**
1585.984	*L. ?thomsoni*	CC	Rp4	2.9	1.5	1.5	1.2??	1.2
1585.917	*L. ?thomsoni*	CC	Lm1 or 2	2.9	1.9	1.7	1.1	1.4
1585.918	*L. ?thomsoni*	CC	Lm1 or 2	2.6	1.8	1.5	1.2	1.5

v.

Chiroptera Blumenbach 1779

Microchiroptera Dobson 1875

Discussion—four upper molars, two from each locality, are referred to the Chiroptera. This referral is based on the well-developed, W-shaped ectoloph found on all these teeth. Other groups known from the Chadronian with similarly developed ectolophs include the soricids and proscalopids, but the well-developed talon of soricids such as *Domnina* is very different (see *Domnina* description) and the overall tooth shape and aspect of the cusps is different from proscalopids such as *Oligoscalops,* which has longer molars with sharper, more bladelike cusps and jagged cuspules along the pre- and postprotocristae. By contrast, the shape and appearance of these four teeth is very similar overall to other North American Tertiary chiropterans such as *Wallia*, *Chadronycteris,* and *Karstala*. Based on their size and morphology, these four molars appear to represent three different taxa.

Gen et sp. indet. 1

Fig. 5.9 A

Referred specimens—

Horse Locality: P2113.769, LM1 or 2; P2478.005, RM1 or 2

Description—The two molars from the Horse Locality are similar in size and shape and appear

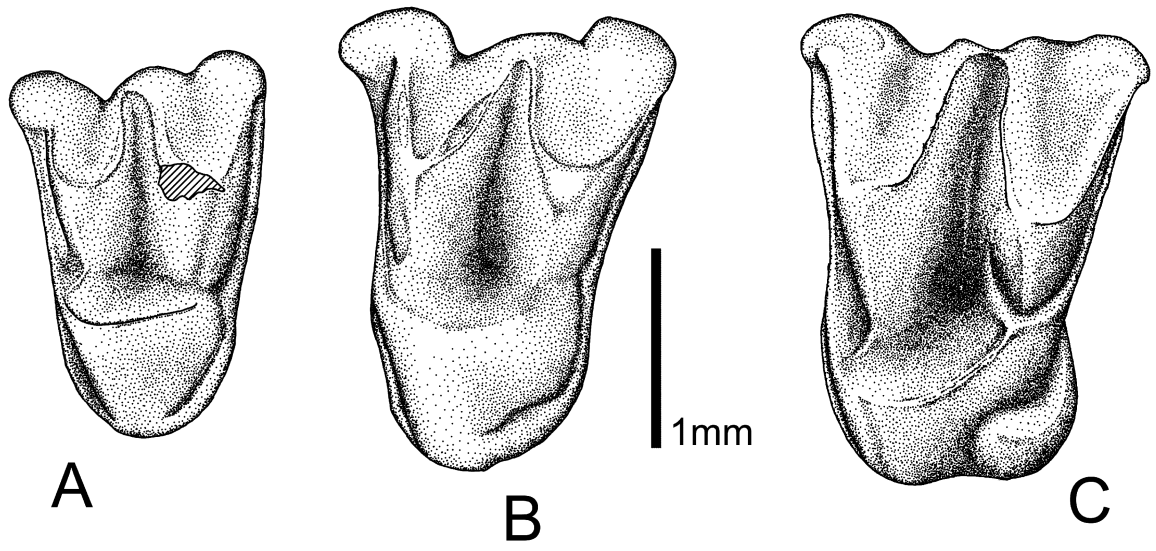


Figure 5.9—Cypress Hills Chiroptera. A, Gen. et sp. indet 1, LM1 or 2 P2113.769; B, Gen. et sp. indet 2, Lm1 or 2 P1585.979; C, Wallia sp. LM1 or 2 P1585.978.

to be conspecific. Both have a well-developed, W-shaped ectoloph. P2478.005 is rather worn and abraded, and is missing the posterobuccal corner of the tooth; its visible morphology is the same as P2113.769.

The overall tooth shape is moderately elongate buccolingually, with a relatively square buccal margin and a narrower, rounded lingual margin (Fig. 5.9A). The protocone is triangular and crescentic, and angles anteriorly, positioned just posterior to the paracone. The preprotocrista runs buccally into the well-developed paracingulum, which extends to the base of the parastyle. The parastyle is hook-shaped (inflected) and continuous with the ectoloph. P2113.769 also has a narrow anterior cingulum along the base of the anterior face of the protocone, which does not connect with the preprotocrista/paracingulum. The posterior cingulum is slightly wider, but there is no hypocone or talon. The postprotocrista extends toward the metacone but ends, leaving a shallow notch between the end of the postprotocrista and the metacone. There is a very small, low paraloph connecting the base of the paracone to the preprotocrista, but no metaloph. At the location of the gap between the postprotocrista and the metacone there is a slight irregularity in

the posterior cingulum, which rises towards the end of the postprotocrista before continuing into the very narrow metacingulum up to the base of the metastyle. The buccal margin of the tooth is indented corresponding to the gaps in the 'W', with the anterior indent being slightly deeper; the buccal side of the stylar shelf is open. The central valley is deep and smooth.

Discussion—These teeth differ from *Chadronycteris,* the only other chiropteran described from the Chadronian of North America, in the open buccal shelf (the buccal shelf of *Chadronycteris* is closed between the mesostyle and metastyle), the gap between the postprotocrista and the metacone (the postprotocrista of *Chadronycteris* reaches the metacone) and the deep central valley (the central valley of *Chadronycteris* is described as shallow.) They are also smaller than reported *Chadronycteris*. They differ from *Wallia* and *Karstala* in their lack of a hypocone. They differ from *Primonatalus* (and all natalids) in the absence of an anterior crest on the mesostyle. The lack of hypocone and metaloph, the gap between postprotocrista and metacone, and the weak paraloph are reminiscent of some *Myotis* (lacks hypocone, metaloph and paraloph),

Gen. et sp. indet 2

Fig. 5.9 B

Referred Specimen—

Calf Creek Locality: P1585.479, LM1 or 2.

Description—P1585.479, from the Calf Creek Locality, is very similar to the two teeth from the Horse Locality described above, except that it is larger, roughly 20% longer and 25% wider (Fig. 5.9B). It shows the same gap between the postprotocrista and the metacone, though there is a very faint metaloph which diverges buccally just before the end of the postprotocrista, running to

the metacone. The paracingulum is narrower relative to the rest of the tooth than in the Horse Locality taxon. The posterior cingulum is somewhat broader posterior to the protocone, but there is no true hypocone; the posterior cingulum is confluent with the metacingulum, but does not rise to approach the end of the postprotocrista as in the Horse taxon.

Discussion—it seems reasonable to assume that this species and the smaller Horse taxon represent members of the same genus, probably different species given the large size difference between them.

Molossidae

Wallia Storer 1984

Range (geographic and temporal)—Uintan to Chadronian of Saskatchewan;

Diagnosis—(from Storer, 1984b) Molars strongly dilamdodont; upper molars with oblique postprotocrista, indistinct para- and metaconule, large, low hypocone except in M3, strong preprotocrista forming anterior shelf reaching to strongly inflected parastyle.

Wallia sp.

Fig. 5.9 C

Referred specimen—

Calf Creek Locality: P1585.478, LM2

Description—The other chiropteran tooth from the Calf Creek, P1585.478 (Fig. F.9zC), is similar in size to P1585.479, though it is somewhat longer. It has the same W-shaped ectoloph with hook-shaped meta- and parastyles, anteriorly-angled protocone, and lingual indentations, but

differs from the previous three in several ways: most notably, it has a well-developed, conical hypocone, whereas the other chiropterans described here have at most a slight swelling of the posterior cingulum at the location of the hypocone; also, the postprotocrista splits and curves around the anterior (metaloph) and posterior faces of the metacone (metacingulum), whereas the other teeth have no significant metaloph. There is a very small, low anterior cingulum on the anterior face of the protocone, separate from the preprotocrista. The preprotocrista is confluent with the paracingulum, which runs anterolingual in a relatively broad shelf across the front of the paracone, to join the parastyle. There is a very slight indication of a paraloph diverging from the preprotocrista to run directly to the paracone. The anterior indentation in the buccal margin of the tooth is similar to those in the other teeth, but there is no corresponding posterior indentation; the posterior external fossette is rather shallow compared to the anterior one, and the metastyle overhangs the posterior cingulum

Discussion—P1585.478 is very similar to the M2 described by Storer (1984b) for *Wallia scalopidens* from the Uintan-aged Swift Current Creek Local Fauna; they share the conical hypocone with a narrow crest extending lingually along a moderate talon; broad paracinglum confluent with preprotocrista; short but not extremely short paraloph; similar buccal margins, with a shallow posterior external fossette. It is about 20% longer anteroposteriorly and 10% wider buccolingually, being less transversely compressed than the Swift Current Creek *Wallia*. The metaloph of P1585.478 runs into the central valley rather than joining the lingual edge of the metacone as it does in *W. scalopidens*, and the hypocone is taller and more conical than in *W. scalopidens*. However, P1585.478 still fits easily within the diagnosis given by Storer (1984b) for the genus, and is far more similar to *Wallia* than any other North American Eocene, Oligocene, or Miocene fossil chiropterans described in the literature. It differs from

Chadronycteris (Chadronian of Nebraska), and *Karstala* and *Primonatalus* (both from Hemingfordian of Florida) in the development of the hypocone, as well as lacking the buccal closure of the stylar shelf found in *Chadronycteris,* the unique structures of the mesostyle and postprotocrista of *Primonatalus,* and the structure of the posterior cingulum and metacingulum, which are confluent in *Karstala* (in *Wallia* the metacingulum is confluent with the postprotocrista).

Wallia was described by Storer (1984b) from the Uintan of the Cypress Hills Formation (Swift Current Creek Local Fauna). Storer's original description included a single lower molar with clear talpoid affinities, however the genus was based on the upper M1; like most Cypress Hills material, the diagnosis was based on a collection of isolated molars from the same site. Storer (1984b) stated "If only the upper dentition of *Wallia* were known, it would be difficult to exclude it from the Palaeochiropterygoidea." However, the validity of the association of the lower, talpoid molar with the uppers is unclear, given the very low numbers of specimens described. Legendre (1985) observed that the features of the *Wallia* uppers were easily accommodated within the chiropteran family Molossidae, leaving the lower, talpoid molar described but nameless. Most subsequent workers have followed this placement. No talpoid lower molars were found at either the Calf Creek or the Horse Locality.

Table 5.9—Measurements for Chiroptera from the Calf Creek and Horse Localities. All measurements are in mm.

Specimen Number	Genus	species	Locality	Tooth position	AP length	Ant width	Post width	LAH	LBH
P2113.769	indet.	sp. 2	H	LM1 or 2	1.37	1.95	2.03	0.89	0.92
P2478.005	indet.	sp. 2	H	RM1 or 2	x	2.05	x	0.71	0.97
P1585.979	indet.	sp. 1	CC	LM1 or 2	1.76	2.50	2.47	1.16	1.13
P1585.978	*Wallia*	sp.	CC	LM2	1.84	2.50	2.42	1.26	1.21

Chapter 6

Discussion

i. Calf Creek and Horse Local Faunas—Comparison

The insectivore faunas from the Calf Creek and Horse Localities of the Cypress Hills are taxonomically diverse, and show few significant changes over the geologically brief time that separates the two sites. The genera and species identified in this study are shown in Table 6.1. All common taxa are shared, although the Horse Local Fauna lacks several rare taxa known from the Calf Creek, most likely due to the somewhat smaller collections from that site.

Table 6.1—Insectivore faunas of the Calf Creek and Horse Localities; compare with tables 2.1 and 2.2. Taxa in bold represent new identifications.

Insectivores of the Calf Creek Local Fauna	**Insectivores of the Horse Local Fauna**
Lipotyphla Apternodontidae *Apternodus* sp., **possibly *A. baladontus*** Geolabididae *Centetodon* ***chadronensis*** Soricidae *Domnina* ***thompsoni*** Oligoryctidae *Oligoryctes* ***altitalonidus*** Micropternodontidae *Micropternodus* ***strophensis*** *Micropternodus* **cf. *montrosensis*** Incertae sedis *Cryptoryctes kayi* Leptictida Leptictidae *Leptictis acutidens* *Leptictis* ***thomsoni*** *Leptictis* ***wilsoni*** Apatotheria Apatemyidae *Sinclairella* ***dakotensis*** *Apatemys* sp. Chiroptera *Wallia* sp. **Gen indet. sp. 1**	**Lipotyphla** **Apternodontidae** ***Apternodus* sp., possibly *A. baladontus*** **Geolabididae** ***Centetodon chadronensis*** **Soricidae** ***Domnina thompsoni*** **Oligoryctidae** ***Oligoryctes altitalonidus*** **Micropternodontidae** ***Micropternodus strophensis*** Incertae sedis ***Cryptoryctes kayi*** Leptictida Leptictidae *Leptictis* ***acutidens*** *Leptictis* ***wilsoni*** **Chiroptera** **Gen indet. sp. 2**

At the beginning of the current research, two possible specific distinctions between the faunas of the two sites were identified, in the species of *Leptictis* and *Micropternodus* present at each site. Subsequent work has confirmed some variation in both these genera between the two sites but the most common species of each genus are the same at both sites.

The majority of the *Leptictis* from both sites is now identified as *L. acutidens;* a single specimen of *L. wilsoni* has also been identified from each site. *Leptictis thomsoni* is identified from the Calf Creek Locality but not from the Horse Locality.

The common species of *Micropternodus* at both sites is currently identified as *M. strophensis*, based on features of the M1s from the Calf Creek Locality and a P4 from the Horse Locality. However, the distinctions between *M. borealis* and *M. strophensis* are slight and they may be conspecific, in which case *M. borealis* is the senior synonym. There appears to be a slight morphological difference between lowers from the two sites in the form of a minute shelf on the buccal surface of the Calf Creek *Micropternodus,* absent from the Horse *Micropternodus.* Early estimates of crown-height differences between the *Micropternodus* lowers from the two sites were not borne out by measurements of unworn specimens; however, three specimens from the Calf Creek did appear, on measurement, to be significantly larger than typical for *Micropternodus strophensis* or *M. borealis.* They fall in the size-range of *M. montrosensis,* although, because that species is based on lowers and the large specimens from the Calf Creek are all uppers, a direct comparison is not possible.

Six taxa were found in the Calf Creek Local Fauna that have not been identified in the Horse Local Fauna; one taxon from the Horse is not known from the Calf Creek. Most striking is the absence of the apatemyid *Sinclairella* from the Horse Locality. Although *Sinclairella* is a relatively rare taxon at the Calf Creek Locality, at least five specimens have been recovered,

making it more abundant than *Domnina thompsoni*, and on par with *Leptictis ?thomsoni*. It is surprising that not even one tooth has been recovered from the Horse; of the taxonomic differences between the insectivores of the two sites, the absence of *Sinclairella* from the Horse Locality seems to be the most likely to represent an actual difference rather than an effect of collection size. All known specimens and possible specimens of *Leptictis thomsoni* also come from the Calf Creek Locality, but while the numbers are similar to *Sinclairella,* the certainty of the identifications is weaker, and it seems possible that specimens of *Leptictis thomsoni* might have been misidentified as *L. acutidens* in the Horse Local Fauna*,* whereas misidentification is unlikely for *Sinclairella*. Thus it is less clear if the absence of *L. thomsoni* from the Horse Locality is a real specific difference between the two sites or merely an artefact of preservation and collection size.

The difference in collection size seems likely to be behind the remaining differences between the Horse Local Fauna and the Calf Creek Local Fauna: the different chiropteran taxa, the two specimens of *Micropternodus* cf. *montrosensis*, and the single upper of *Apatemys?* from the Calf Creek. The only taxon known from the Horse Local Fauna but not from the Calf Creek is the bat taxon (gen. indet; sp. 2). In the case of the Calf Creek and Horse local faunas, age differences within the middle Chadronian cannot be reliably distinguished based on insectivores alone, certainly not in taxa common enough to be considered reliable index fossils.

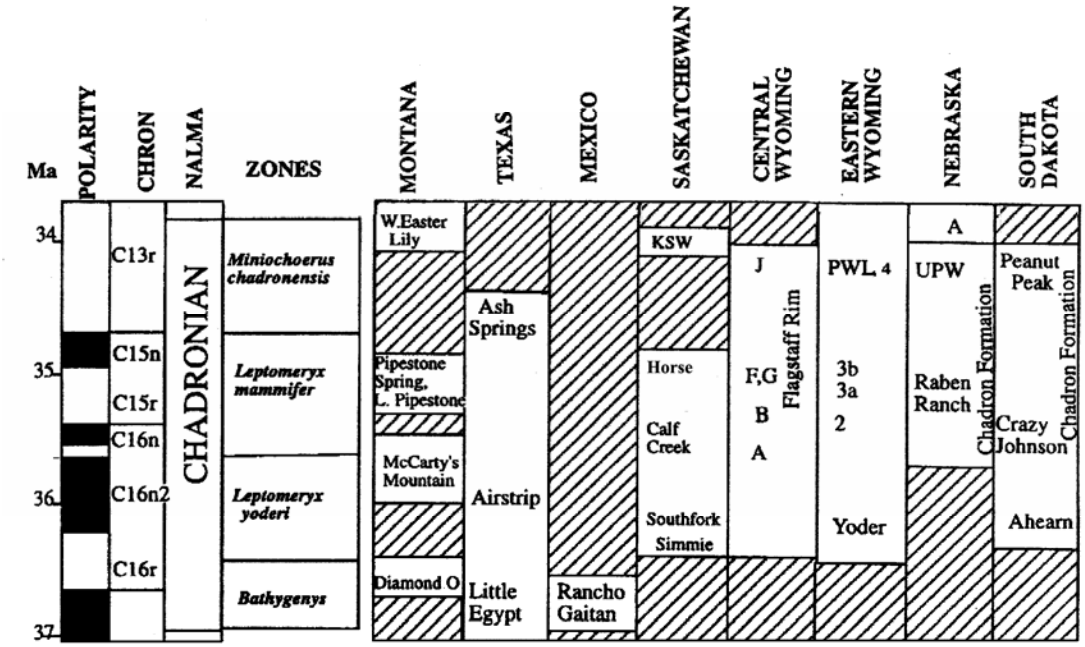


Figure 6.1—Subdivisions of the Chadronian and correlation of various Chadronian faunas, from Prothero and Emry (2004). *Bathygenys* zone equivalent to earliest Chadronian; *Leptomeryx yoderi* zone equivalent to late early Chadronian; *Leptomeryx mammifer* zone equivalent to middle Chadronian; *Miniochoerus chadronensis* zone equivalent to late Chadronian.

ii. Comparison with other localities

Prothero and Emry (2004) list the two insectivore species that first appear in the late early Chadronian and range into the middle Chadronian, *Centetodon chadronensis* and *Sinclairella dakotensis;* the problems concerning the age range of *Sinclairella* have been discussed previously. The only "insectivore" mentioned as limited to the middle Chadronian is *"Frictops emryi",* a leptictid nomen nudum which may be the same as one of the *Leptictis* species present in the Cypress hills (see discussion in Chapter 5.iv). Prothero and Emry (2004) do not list any insectivores indicative of the late Chadronian.

The number of Chadronian faunas with a well studied, published insectivore component

is relatively limited. These include the Pipestone Springs Local Fauna of Montana (Tabrum et al., 1996), the Flagstaff Rim Faunas of Wyoming (Emry, 1992), the Raben Ranch Local Fauna of Nebraska (Ostrander 1983, 1987), and the Medicine Pole Local Fauna of North Dakota (Kihm and Schumaker, 2004), as well as the less extensive published faunas from the Peanut Peak member of the Big Badlands of South Dakota (Clark and Beerbower, 1967) and the Vieja Group of Texas (Novacek, 1976; Wilson, 1986); see Table 6.2 for faunal lists, Fig. 6.2 for locations. The less extensive faunas are both from older publications, and may not reflect the current state of knowledge with regard to these localities. All the faunal lists discussed here have been updated based on the revisions of *Centetodon* (Lillegraven et al. 1981) and apternodontids and oligoryctids (Asher et al. 2002), wherever applicable. The higher taxonomic designations have also been adjusted to match those used elsewhere in this work, for consistency and to avoid confusion.

The Pipestone Springs assemblage has been considered the "type locality" of the middle Chadronian (Tabrum et al., 1996), and it shows strong resemblances to the Calf Creek and Horse insectivore faunas. They share key middle Chadronian insectivore taxa such as *Leptictis acutidens* and *L. thomsoni* (at Calf Creek but not at Horse Locality) and *Domnina thompsoni*. The species of *Micropternodus* identified is different, but if *M. strophensis* is in fact a junior synonym of *M. borealis* this difference becomes apparent rather than real; the type locality of *M. strophensis* is also from southwestern Montana. In particular, the *Apternodus* species present at the Cypress Hills sites, though it cannot be identified beyond a doubt, is most likely *A. baladontus,* which is known only from the Pipestone Springs area. Given this connection between the two areas, it is interesting that the *Centetodon* species are different, since *C. kuenzii* is also known only from the Pipestone Springs area. *Oligoryctes cameronensis* is present at

Table 6.2—Insectivore faunas of the Pipestone Springs Locality, Montana; Flagstaff Rim, Wyoming; Raben Ranch Locality of Nebraska, Big Badlands of South Dakota, Medicine Pole Fauna of North Dakota, and Little Egypt Local Fauna of Texas.

Pipestone Springs, Montana (From Tabrum, Prothero, and Garcia, 1996, updated by Asher et al., 2002)	**Flagstaff Rim, Wyoming** (From Emry, 1992)	**Raben Ranch, Nebraska** (Ostrander, 1983, 1987)
Insectivora Geolabididae *Centetodon kuenzii* *Centetodon magnus* Micropternodontidae *Micropternodus borealis* Apternodontidae *Apternodus mediaevus* *Apternodus baladontus* Oligoryctidae *Oligoryctes altitalonidus* *Oligoryctes cameronensis* Soricidae *Domnina thompsoni* Proscalopidae *Oligoscalops*? new species Incertae sedis *Cryptoryctes kayi* Leptictida Leptictidae *Leptictis acutidens* *Leptictis thomsoni*	Insectivora Apternodontidae *Apternodus brevirostris* *Apternodus gregoryi* Oligoryctidae *Oligoryctes altitalonidus* *Oligoryctes cameronensis* Leptictidae "*Fricktops emryi*" Sespedectidae *Ankylodon* sp. Geolabididae *Centetodon chadronensis* Apatotheria Apatemyidae *Sinclairella* sp. Chiroptera sp.	Insectivora Geolabididae *Centetodon chadronensis* Sespedectidae *Ankylodon* sp. Soricidae *Domnina gradata* *Domnina thompsoni* Proscalopidae *Oligoscalops* Apternodontidae *Apternodus ?iliffensis* *Oligoryctes cameronensis* Micropternodontidae *Micropternodus borealis* *Micropternodus montrosensis* Apatemyidae *Sinclairella dakotensis* ?Pantolestidae, gen. et sp. indet. Chiroptera: *Chadronycteris rabenae* Leptictida Leptictidae *Leptictis acutidens*
Chadron Formation, Peanut Peak Member, Big Badlands, South Dakota (Clark and Beerbower, 1967). No microfauna was given for the other members.	**Medicine Pole Local Fauna, North Dakota (Kihm and Schumaker, 2004)**	**Vieja Group, Texas Little Egypt Local Fauna (Novacek, 1976; Wilson, 1986)**
Leptictida Leptictidae *Leptictis dakotensis* Lipotyphla Oligoryctidae *Oligoryctes altitalonidus* (type) Apternodontidae *Apternodus "mediaevus"* (specimen lost, could not be evaluated by Asher et al. 2002) Micropternodontidae *Clinopternodus gracilis* Geolabididae *Centetodon chadronensis* (ID of Lillegraven et al., 1981) Apatotheria Apatemyidae *Sinclairella dakotensis* (type)	Leptictida Leptictidae *Leptictis* cf. *L. acutidens* Lipotyphla Soricidae *Domnina* large sp. (new) *Domnina* cf. *D. thompsoni* Apternodontidae *Apternodus* sp. Oligoryctidae *Oligoryctes* cf. *O. cameronensis* Geolabidiade *Centetodon chadronensis* Micropternodontidae *Micropternodus* cf. *M. borealis* Incertae sedis *Cryptoryctes* sp. Apatotheria Apatemyidae *Sinclairella* sp. Chirotpera 2 species	Leptictida Leptictidae *Leptictis wilsoni* Lipotyphla Geolabididae *Centetodon* Apternodontidae *Apternodus*

Pipestone Springs and absent from Calf Creek and Horse, as are *Oligoscalops, Ankylodon,* and *Centetodon magnus*; based on stratigraphic ranges from the Flagstaff Rim (see below) these taxa might be indicators of a later age for the Pipestone Springs Local Fauna. Conversely, apatemyids such as *Sinclairella* and even *Apatemys* are known from the Calf Creek, but seem to be absent from the south-west Montana faunas entirely, including those older than the Pipestone Springs fauna (Tabrum et al., 1996). The Pipestone Springs Local Fauna is generally correlated as slightly younger than the Calf Creek Local Fauna, (Storer, 1996; Prothero and Emry, 2004; see Figure 6.1.) while the Horse Local Fauna is suggested to be of the same age (Prothero and Emry, 2004; Figure 6.1) or slightly later (McDougall, 1995). If the absence of *Ankylodon, Oligoscalops*, and *Oligoryctes cameronensis* from the Cypress Hills were in fact age- rather than geography-related, this would argue for an earlier date for the Horse Locality relative to the Pipestone Springs. However, the non-insectivore material seems to favour the later date within the Middle Chadronian for the Horse Locality, and the geographic and temporal ranges of genera like *Ankylodon* and *Oligoscalops* are too poorly-understood to make a clear-cut argument for age based on their absence from the Calf Creek and Horse Localities. The age-correlations suggested by Storer (1996) remain credible: that the Calf Creek Local Fauna is slightly older than the Pipestone Springs and that the Horse Locality is of the same age as the Pipestone Springs or slightly younger.

Comparison of the Calf Creek and Horse Local Faunas with taxa recovered from the Flagstaff Rim of Wyoming is particularly interesting because the Flagstaff Rim taxa have been recovered with fairly precise stratigraphic information which allows the construction of stratigraphic ranges for individual taxa (Emry, 1992). As noted by Storer (1996), the Calf Creek Local Fauna correlates best with the lower part of the White River Formation at Flagstaff Rim,

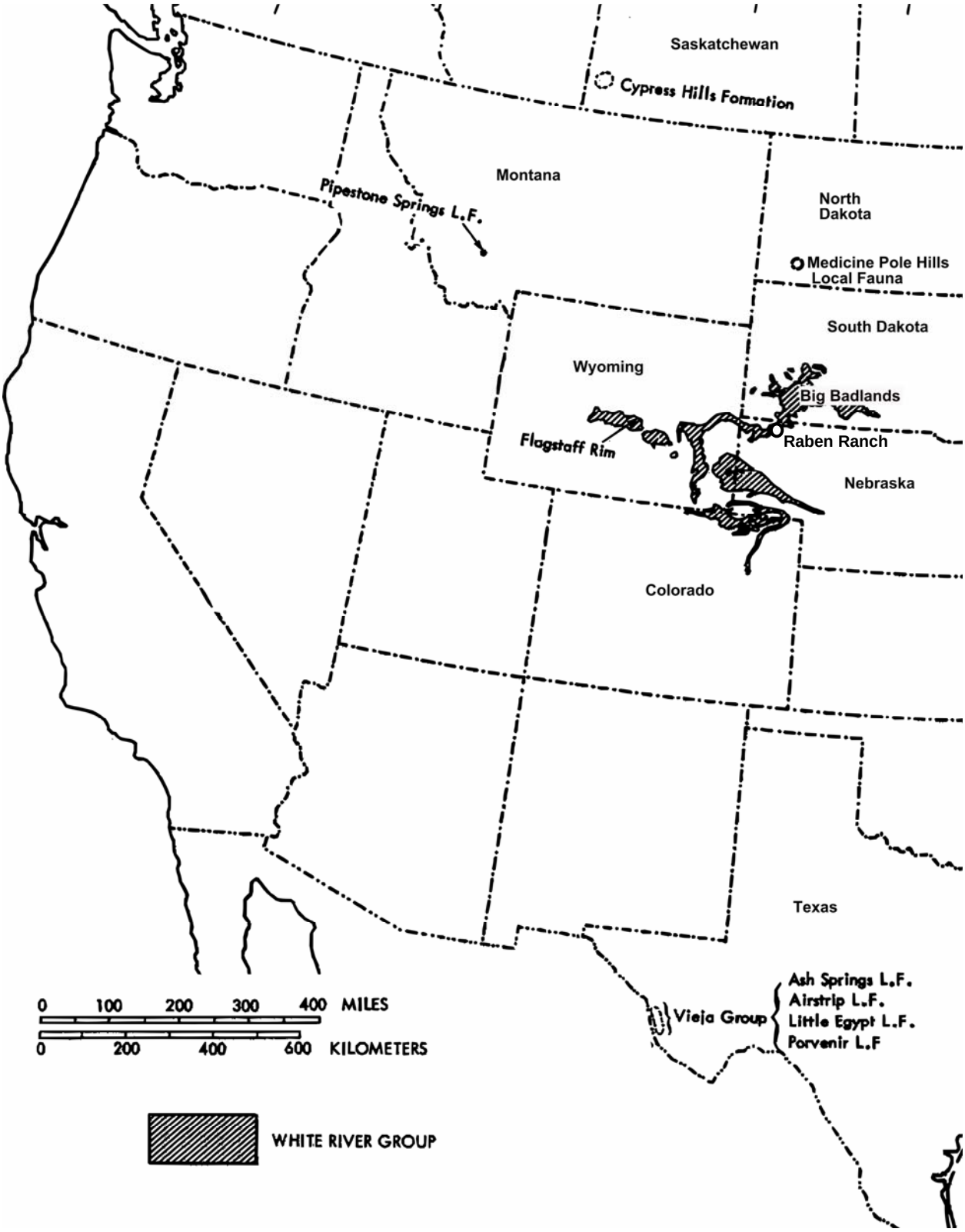


Figure 6.2—Map of western United States and southern Canada, showing localities discussed in the text. Modified from Prothero and Emry (2004).

and the new insectivore identifications do not change this. The best fit of insectivore taxa with the Calf Creek Local Fauna occurs between 150-220 feet (46 to 67 m) above the base of the White River Formation at Flagstaff Rim, the range in which *Sinclairella* overlaps with *"Fricktops emryi"* at the Flagstaff Rim, assuming *"Fricktops"* is equivalent to one of the leptictids from the Calf Creek Locality (as discussed in Chapter 5.iv). This range is equated with the lower half of the middle Chadronian (*Leptomeryx mammifer* zone) by Prothero and Emry (2004). The Horse Locality insectivores may correlate best slightly higher in the section, between 220-320 feet (67 to 97 m), after the disappearance of *Sinclairella* from the Flagstaff Rim, but still during the range of *Oligoryctes altitalonidus*, levels correlated with the upper part of the middle Chadronian by Prothero and Emry (2004) but still lower than the latest middle Chadronian. Several middle Chadronian species absent from the Calf Creek and Horse Localities are found at Flagstaff Rim only above 300 ft (91 m, latest middle Chadronian of Prothero and Emry, 2004), including *Oligoryctes cameronensis* and *Ankylodon,* as well as *Apternodus gregoryi* and *Apternodus brevirostris*. No lower occurrence of *Apternodus* is reported by Emry (1992). Again, the insectivores alone appear to suggest a somewhat younger age for the Horse Locality when compared to the Flagstaff Rim.

The Raben Ranch Local Fauna of Nebraska is viewed by Prothero and Emry (2004, Fig. 6.1) to lie between the Calf Creek and Horse Local Faunas in age, and it shares key taxa such as *Leptictis acutidens, Centetodon chadronensis*, and *Domnina thompsoni* with the Cypress Hills faunas. It contains several taxa which occur higher in the Flagstaff Rim than any present in the Calf Creek or Horse Local Faunas, such as *Oligoryctes cameronensis* and *Ankylodon*, but also includes *Sinclairella,* which is found only in the lower part of the Flagstaff Rim. The bat taxon,

Chadronycteris, described from the Raben Ranch, is different than any of the bats found at the Cypress Hills fauna. The *Micropternodus* species identified by Ostrander (1987) is *M. borealis*, but the validity of this identification is in question (see *Micropternodus* discussion). Ostrander (1987) identified the Raben Ranch *Apternodus* as *A. iliffensis;* Asher et al. (2002) feel this is questionable due to the difficulty of identifying isolated molars of *Apternodus* to species, but based on Ostrander's description it appears reasonable, and can probably be viewed as having similar weight to the tentative identification of *A. baladontus* from the Calf Creek and Horse Local Faunas. The Raben Ranch Local Fauna is probably best viewed as younger than the Calf Creek, but of similar age to the Horse and the Pipestone Springs Local Faunas.

The only other significantly complete Chadronian insectivore fauna is the Medicine Pole Fauna of North Dakota (Kihm and Schumaker, 2004). It is very similar to the Calf Creek and Horse Local Faunas, again sharing *Centetodon chadronensis*, *Leptictis* cf. *L. acutidens,* and *Domnina thompsoni*. It has *Sinclairella* but also *Oligoryctes cameronensis*, a "later" taxon at the Flagstaff Rim. Like the Calf Creek and Horse Local Faunas, the Medicine Pole Fauna contains *Cryptoryctes* humeri and only one of the "candidate" dentitions, *Micropternodus*. One of the chiropteran taxa from the Medicine Pole Fauna may be the same as Chiroptera gen. indet sp. 1, from the Calf Creek Local Fauna, although a full comparison has not been made (Kihm, personal communication 2007). The Medicine Pole Local Fauna may be slightly younger than the Calf Creek and the Horse local faunas, based on the presence of *O. cameronensis*; description of the non-insectivores from the Medicine Pole Local Fauna will likely clarify the age of this fauna further.

Clark and Beerbower (1967) discuss the Chadron Formation of the Big Badlands of South Dakota, but the only microfauna comes from the upper Peanut Peak Member, correlated

by Prothero and Emry (2004) with the late Chadronian. It contains *Centetodon chadronensis* but not *Leptictis acutidens* or *Domnina thompsoni*, and is also the type locality for *Oligoryctes altitalonidus* and *Sinclairella dakotensis,* both of which are found low in the Flagstaff Rim; it is clear that the age-ranges found at the Flagstaff Rim taxa do not always represent ranges in other areas. With such a limited fauna, it is not clear how many of the differences relate to age or geography, and how many to an incomplete fauna. The presence of *Clinopernodus* and *Leptictis dakotensis* do suggest a rather different, probably younger, age for the Peanut Peak fauna, however.

There are very few insectivores published from the Vieja group of Texas, and only one of Chadronian age identified to species in the published literature. This is *Leptictis wilsoni,* from the earliest Chadronian Little Egypt Local Fauna, and it is the only species of insectivore shared between the Texas and Cypress Hills faunas. The Little Egypt Local Fauna appears, based on other taxa, to be older than the Calf Creek and the Horse Local Faunas, so the identification of *L. wilsoni* from the Cypress Hills extends not only the geographic but also the temporal range of the species.

The new identifications of the insectivores from the Calf Creek and Horse Local Faunas do not substantially challenge previous estimates of the ages of the two sites. The Calf Creek still appears likely to be somewhat earlier within the middle Chadronian than many of the other middle Chadronian localities. The absence of *Oligoscalops*, *Oligoryctes cameronensis*, and *Ankylodon* may indicate a slightly earlier age for the Horse Locality than has been suggested elsewhere (eg. McDougall, 1995; Storer, 1996), but the non-insectivore identifications do not support this interpretation; further description of more elements of the Horse Local Fauna will hopefully shed light on its precise age.

The preceding comparisons illuminate various things about the insectivores of the middle Chadronian. Several taxa can be seen to have a wide range in time and space and are found in most well-sampled middle Chadronian faunas: *Leptictis acutidens, Centetodon chadronensis,* and *Domnina thompsoni.* The ranges of other taxa, such as *Oligoryctes cameronensis*, *Oligoscalops, Domnina gradata* and *Leptictis thomsoni*, appear to be more restricted, though it is still difficult to discern which occurrences reflect temporal ranges, geographic ranges, or incomplete sampling.

Although *Sinclairella* has a fairly broad temporal range (late early Chadronian to Orellan), it seems to show a geographic distribution of consistent occurrences in the east (the Dakotas and Nebraska), patchy occurrence in the mid-west (Wyoming, Saskatchewan, and Colorado), and absence from the well-known sites of western Montana.

Oligoryctes cameronensis appears higher than *O. altitalonidus* at the Flagstaff Rim, but the two co-occur at Pipestone Springs; while the absence of *O. cameronensis* from the Calf Creek Local Fauna might indicate an early date for this fauna, the absence of *O. cameronensis* from the Horse is more certainly a geographic limitation, since the Horse is likely of the same age or later than the Pipestone Springs Local Fauna. At the same time, *O. cameronensis* is the only species of *Oligoryctes* recorded from the Raben Ranch Local Fauna of Nebraska, which might suggest a slightly more southern range for *O. cameronensis*, with a broad area of overlap with *O. altitalonidus* in Montana and Wyoming but not reaching as far north as Saskatchewan.

Other taxa, like *Oligoscalops,* and *Ankylodon*, are not sufficiently well known or understood, particularly at the species level, to make broad statements about their range or occurrence.

The insectivores of the Calf Creek and Horse Local Faunas agree well with other faunas

from the middle Chadronian, and no new species are suggested here except in the case of the chiropterans. However, the specific faunal mix shared by the Calf Creek and Horse Localities is unique, and the two sites are much more similar to each other at the species level than to faunas from any other region. Only in the case of the Medicine Pole Local Fauna are more than half the taxa shared with the Calf Creek Local Fauna (5 of 9). The Pipestone Springs Fauna has the highest overall number of insectivore species in common with the Calf Creek (6 of 12), although the agreement is lower (5 of 12) for the Horse Local Fauna due to the absence of *Leptictis thomsoni* from the Horse. Of the well known middle Chadronian insectivore faunas the Raben Ranch fauna has the lowest proportion of species shared with the Calf Creek and Horse Local Faunas, at 5 of 12 species. Agreement at the genus level is higher, with 7 of 8 genera from the Pipestone Springs Locality present at both Calf Creek and Horse Localities, and 8 of 8 from the Medicine Pole Locality, but again agreement is lowest for the Raben Ranch fauna, at 7 of 10 genera shared (6 for the Horse Local Fauna). In contrast, all the species known from the Horse Locality except the chiropteran taxon (gen. et sp. indet. 1) are present at the Calf Creek, (8 of 9 species.) Although the numbers above ignore issues of faunal completeness, they do give a crude impression of similarity and differences between faunas; unsurprisingly the most northern faunas (Montana and North Dakota) show greater similarity with the Cypress Hills faunas than the more southern faunas from Wyoming and Nebraska; however, the specific mix of each area is unique. The Cypress Hills faunas are no more distinct than the various American faunas are from each other, but they are distinctly more similar to each other than to faunas from other areas.

In general it is clear that precise, species-level identifications and large samples wherever possible are critical for a detailed understanding of the fauna of a locality and its relationship to other similar-aged sites. Sites such as the Calf Creek and Hose Localities are invaluable in that

the breadth of taxa recoverable most likely represents the majority of vertebrates living in the area at the time, providing a high-resolution picture of the fauna of the area. Once detailed taxonomic identification has occurred, these faunas can be compared with other sites, as well as modern environments, to assess characteristics of age, environment, ecological structure, and perhaps even climate. But to allow for these more advanced deductions, large collections must be amassed and identified in detail; thousands of specimens must be accrued, and the differences in faunal richness between the Horse and the Calf Creek Local Faunas suggest that even a fauna in excess of 2500 specimens, as at the Horse Locality, is not revealing the total species richness that may be present in the fossil record. Even the impressive Calf Creek collections contain several rare taxa for which only a few teeth, far less than a complete dentition, are known.

iii. Future work:

Other highly fossiliferous Chadronian localities are known from the Cypress Hills Formation. The Bud Locality, located along the same Highway 614 that runs through the Horse Locality, is a thick, highly fossiliferous roadcut exposure from which a significant Chadronian and somewhat smaller Orellan fauna has been recovered. However, intensive screening and identification of taxa from the site has not yet taken place, and its similarities to and differences from the Calf Creek and Horse Local Faunas cannot yet be assessed. Similar work remains to be done on the fauna from the Irish Springs Locality, located some 20 km east of the Horse Locality, where sediment matrix has been collected and screened but not yet picked for fossils.

The current research has brought the study of the taxonomy of the Calf Creek Local Fauna much closer to completion, though the brontotheres are in need of revision and some smaller families, such as the camels and merycoidodonts, have not yet been described. The

descriptive work on the Horse Local Fauna is just beginning. More detailed studies on the Calf Creek Local Fauna, examining questions of environment, climate, taphonomy, and more, can now be contemplated.

Construction of rarefaction curves for the entire faunas of both the Calf Creek and Horse Localities could prove valuable for estimating faunal completeness at both localities, potentially providing another line of evidence with regards to whether the faunal differences between the two sites are actual or merely the result of sampling. However, for such curves to be meaningful, accurate specific identification of all taxa is required; a reasonable rarefaction curve could probably be constructed for the Calf Creek based on current identifications, despite the problem areas mentioned above, but specific identifications for the Horse Local Fauna would need to be completed.

At the same time, dozens of highly fossiliferous microsites are known from the Cypress Hills Formation, stretching from Uintan to Hemingfordian in age, and detailed faunal reviews have been completed for only a handful of them. Much remains to be done at many of these sites in terms of processing matrix and isolating fossil remains, before even beginning the taxonomic work or addressing the larger questions mentioned above that a detailed taxonomy makes possible. The future of palaeontology in the Cypress Hills Formation is rich and exciting indeed.

References

Asher, R. J. 2005. Insectivoran-grade placentals; pp. 50-70 in K. D. Rose and J. D. Archibald (eds.), The Rise of Placental Mammals. Johns Hopkins University Press, Baltimore, Maryland.

Asher, R. J., M. C. McKenna, R. J. Emry, A. R. Tabrum, and D. G. Kron. 2002. Morphology and relationships of *Apternodus* and other extinct, zalamdodont, placental mammals. Bulletin of the American Museum of Natural History 273:1-117.

Asher, R. J.; Novacek, M. J.; Geisler, J. H. 2003 Relationships of endemic African mammals and their fossil relatives based on morphological and molecular evidence. Journal of Mammalian Evolution 10: 131-194.

Asher, R. J.; Emry, R. J.; Mckenna, M. C. 2005. New material of *Centetodon* (Mammalia, Lipotyphla) and the importance of (misisng) DNA sequences in systematic paleontology. Journal of Vertebrate Paleontology 25(4): 911-923.

Barnosky, Anthony D. 1981. A skeleton of *Mesoscalops* (Mammalia, Insectivora) from the Miocene Deep River Formation, Montana, and a review of the proscalopid moles: evolutionary, functional, and stratigraphic relationships. Journal of Vertebrate Paleontology 1(3-4):285-340.

Beck, R., O. Bininda-Emonds, M. Cardillo, F.-G. R. Liu, and A. Purvis. 2006. A higher-level MRP supertree of placental mammals. BMC Evolutionary Biology 6:93

Bell, S. D. 2004. Aplodontid, sciurid, castorid, zapodid and geomyoid rodents of the Rodent Hill Locality, Cypress Hills Formation, southwest Saskatchewan. M. S. thesis, University of Saskatchewan, Saskatoon, Saskatchewan, 167 pp.

Bryant, H. N. 1991. Reidentification of the Chadronian supposed didlephid marsupial *Alloedectes mcgrewi* as part of the deciduous dentition of the canid Hesperocyon. Canadian Journal of Earth Sciences 28(12): 2062-2065.

Bryant, H. N. 1992. The Carnoviora of the Lac Pelletier Lower Fauna (Eocene: Duchesnean), Cypress Hills Formation, Saskatchewan. Journal of Paleontology 66(5): 847-855.

Bryant, H. N. 1993. Carnivora and Creodonta of the Calf Creek Local Fauna (Late Eocene, Chadronian), Cypress Hills Formation, Saskatchewan. Journal of Paleontology 67:1032-1046.

Butler, P. M. 1948. On the evolution of the skull and teeth in the Erinaceidae, with special reference to fossil material in the British Museum. Zoological Society of London, Proceedings 118:446-500.

Butler, P. M. 1956. The skull of *Ictops* and the classification of the Insectivora. Zoological Society of London, Proceedings 126(3):453-481.

Butler, P. M. 1972. The problem of insectivore classification; pp. 253-265 in K. A. Joysey, T. S. Kemp (eds.), Studies in vertebrate evolution. Oliver and Boyd, Edinburgh, Scotland.

Butler, P. M. 1988. Phylogeny of the Insectivores; pp. 117-141 in Michael J. Benton (ed.) The Phylogeny and Classification of the Tetrapods, Vol. 2: mammals. Oxford University Press, Oxford.

Clark, J. 1936. Excerpts in Scott and Jepsen, The mammalian fauna of the White River Oligocene. Transactions of the American Philosophical Society (New Series)

28:iii-151
Clark, J. 1937. The stratigraphy and paleontology of the Chadron Formation in the Big Badlands of South Dakota. Annals of the Carnegie Museum 25:261-350.
Clark, J., and J. R. Beerbower. 1967. Geology, Paleoecology, and paleoclimatology of the Chadron Formation. Fieldiana: Geology memoirs 5: 21-74.
Clemens, W. A., Jr.1964. Records of the fossil mammal *Sinclairella*, Family Apatemyidae, from the Chadronian and Orellan. University of Kansas Publications, Museum of Natural History 14(17):485-491.
Cook, H. J. 1954. A remarkable new mammal from the Lower Chadron of Nebraska. American Midland Naturalist 52:388-391
Cope, E. D. 1885a. The White River Beds of Swift Current river, Northwest territory. American Naturalist 19(2):163.
Cope, E. D. 1885b. The Vertebrata of the Swift Current Creek Region of the Cypress Hills; Appendix I in McConnell, R. G., Report on the Cypress Hills, Wood Mountain, and Adjacent Country. Geological Survey of Canada, Annual Report, New Series 1 (Part C): 79-85.
Cope, E. D. 1889a. The Vertebrata of the Swift Current River, II. The American Naturalist 23(267):621-633
Cope, E. D. 1889b. Vertebrata of the Swift Current River, no. III. The American Naturalist 23(271):621-633.
Cope, E. D. 1891. On vertebrata from the Tertiary and Cretaceous rocks of the North West Territory, I. —The species from the Oligocene or Lower Miocene beds of the Cypress Hills. Contributions to Canadian Palaeontology 3(1):1-25.
Davis, N. B. 1918. Report on the Clay Resources of Southern Saskatchewan. Canada Department of Mines, Mines Branch, Report 469. 93 pp.
Dawson, G. M. 1875. Report on the geology and resources of the region in the vicinity of the forty-ninth parallel from the Lake of the Woods to the Rocky Mountains. British North American Boundary Commission, Montreal, 378 pp.
Douady, C. J., and E. J. P. Douzery. 2003. Molecular estimation of eulipotyphlan divergence times and the evolution of "Insectivora." Molecular Phylogenetics and Evolution 28: 285-296.
Douglass, E. 1902. Fossil mammalia from the White River Beds of Montana. Transactions of the American Philosophical Society 20:237-279
Douglass, E. 1905. The Tertiary of Montana. Memoirs of the Carnegie Museum, pp. 146-199.
Eberle, J., and Storer, J. E. 1995. *Herpetotherium valens* (Lambe), a didelphid marsupial from the Calf Creek local fauna (Chadronian), Saskatchewan. Journal of Vertebrate Paleontology 15(4)785-794.
Emerson, G. L., C. W. Kilpatrick, B. E. McNiff, J. Ottenwalder, and M. W. Allard. 1999. Phylogenetic relationships of the Order Insectivora based on complete 12S rRNA sequences from mitochondria. Cladistics 15: 221-230.
Emry, R. J. 1992. Mammalian range zones in the Chadronian White River Formation at Flagstaff Rim, Wyoming; pp.106-115 in D. R. Prothero and W. A Bergren (eds.), Eocene-Oligocene Climatic and Biotic Evolution. Princeton University Press, Princeton, New Jersey.
Emry, R. J., L. S. Russell, and P. R. Bjork. 1987. The Chadronian, Orellan, and

Whitneyan North American Land Mammal Ages; pp. 118-152 in M. O. Woodburne (ed.), Cenozoic Mammals of North America. University of California Press, Berkeley, California.

Fox, R. C. 1983. New evidence on the relationships of the Tertiary insectivoran *Ankylodon* (Mammalia). Canadian Journal of Earth Sciences, 20:968-977.

Furnival, G. M. 1946. Cypress Lake map-area, Saskatchewan. Geological Survey of Canada Memoirs 242:1-161.

Galbreath, E. C. 1953. A contribution to the Tertiary geology and paleontology of northeastern Colorado. University of Kansas Paleontological Contributions, Vertebrata 4:1-120.

Gregory, W. K. 1910. The orders of mammals. Bulletin of the American Museum of Natural History 27:1-524

Grenyer, R., and A. Purvis. 2003. A composite species-level phylogeny of the 'Insectivora' (Mammalia: Order Lipotyphla Haeckel, 1866). Journal of Zoology (London) 260:245-257.

Haeckel, E. 1866. Generelle Morphologie der Organismen, vol. 2: Systematische Einteilung in die allgemeine Entwickelungsgeschichte. Reimer, Berlin, Germany, 447 pp.

Holman, J. Alan. 1963. A new rhinophrynid frog from the early Oligocene of Canada. *Copeia,* Canadian Journal of Earth Sciences 1963(4):706-708.

Holman, J. 1968. Lower Oligocene amphibians from Saskatchewan. Quarterly Journal of the Florida Academy of Science 31(4):273-289.

Holman, J. 1972. Herpetofauna of the Calf Creek Local Fauna (Lower Oligocene: Cypress Hills Formation) of Saskatchewan. Canadian Journal of Earth Sciences 9:1612-1631.

Hough, J. 1956. A new insectivore from the Oligocene of the Wind River Basin, Wyoming, with notes on the taxonomy of the Oligocene Tenrecoidea. Journal of Paleontology 30(3):531-541.

Huxley, T. A. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia. Proceedings of the Royal Society of London 43: 649-662.

Jepsen, G. L. 1934. A revision of the American Apatemyidae and the Description of a New Genus, *Sinclairella*, from the White River Oligocene of South Dakota. Proceedings of the American Philosophical Society 74(4)

Kihm, A. J. 2007. Personal communication (email).

Kihm, A. J., and K. K. Schumaker. 2004. The Chadronian Medicine Pole Hills Local Fauna, North Dakota; in J. H. Hartman (ed.), Vertebrate Paleontology of the High Plains—the late Mesozoic-Cenozoic record of North Dakota. University of North Dakota Department of Geology and Geological Engineering Contribution to Geology 54:77-84.

Krishtalka, L., R. J. Emry, J. E. Storer, and J. F. Sutton. 1982. Oligocene multituberculates (Mammalia: Allotheria): youngest known record. Journal of Paleontology 56:791-794.

Kupsch, W. O. 1956. Geology of eastern Cypress Hills Saskatchewan. Saskatchewan Department of Mineral Resources, Report 20. 30 pp.

Lambe, L. M. 1905a. A new species of *Hyracodon* (*H. priscidens*) from the Oligocene of

the Cypress Hills, Assiniboia. Proceedings and Transactions of the Royal Society of Canada, Series 2, 11(section 4): 37-42.

Lambe, L. M. 1905b. Fossil horses of the Oligocene of the Cypress hills, Assiniboia. Proceedings and Transactions of the Royal Society of Canada, Series 2, 11(section 4): 43-52.

Lambe, L. M. 1905c. Vertebrate Paleontology. Summary Report of the Geological Survey Department of Canada for the calendar year 1904. Sessional Paper no. 26:362-371

Lambe, L. M. 1908. The vertebrata of the Oligocene of the Cypress Hills, Saskatchewan. Contributions to Canadian Paleontology 3(4):5-64.

Leckie, D. A., and R. J. Cheel. 1989. The Cypress Hills Formation (Upper Eocene to Miocene): a semi-arid braidplain deposit resulting from intrusive uplift. Canadian Journal of Earth Sciences 26:1918-1931.

Leckie, D. A., and R. J. Cheel. 1990. Nodular silcretes of the Cypress Hills Formation (upper Eocene to middle Miocene) of southern Saskatchewan, Canada. Sedimentology 37:445-454

Leidy, J. 1868. Notice of some remains of extinct Insectivora from Dakota. Proceedings of the Academy of Natural Sciences of Philadelphia, pp. 315-316.

Legendre, S. 1985. Molossides (Mammalia, Chiroptera) cenozoique de l'Ancien et du Nouveau monde; statut systematique; integration phylogenique des donnees. Translated Title: Old and New World Cenozoic molossid bats (Mammalia, Chiroptera); systematic status; phylogenetic integration of data. Neues Jahrbuch fuer Geologie und Palaontologie 170(2):205-227.

Lillegraven, J. A., M.C. McKenna, and L. Krishtalka. 1981. Evolutionary relationships of middle Eocene and younger species of *Centetodon* (Mammalia, Insectivora, Geolabididae) with a description of the dentition of *Ankylodon* (Adapisoricidae). University of Wyoming Publications 45:1-115.

Lillegrave, J. A., and A. R. Tabrum. 1983. A new species of *Centetodon* (Mammalia, Insectivora, Geolabididae) from Southwestern Montana and its biogeographical implications. Contributions to Geology, University of Wyoming 22(1):57-73

Lopatin, A. V. 2002. The earliest shrew (Soricidae, Mammalia) from the Middle Eocene of Mongolia. Paleontological Journal 36(6): 78-87.

Lopatin, A. V. 2004. A new soricomorph insectivore (Soricomorpha, Mammalia) from the Eocene of Mongolia and the Origin of Shrews (Soricidae). Doklady Biological Sciences 401: 144-146.

Lundberg. J. G. 1975. The fossil catfishes of North America. Papers on Paleontology, University of Michigan 11:1-51.

MacDonald, J. R. 1963. The Miocene faunas from the Wounded Knee area of western South Dakota. Bulletin of the American Museum of Natural History 125(3):139-238.

MacPhee, R. D. E. & Novacek, M. J. (1995). Definition and relationships of Lipotyphla; pp. 13-31 in F. S. Szalay, M. J. Novacek, and M. C. McKenna (eds), Mammal phylogeny—placentals. Springer-Verlag, Berlin, Germany.

Martz, L., and D. de Boer. 1999. Digital Terrain Models; pp. 92-94, in K. Func, B. Barry, M. Wilson (eds.), Atlas of Saskatchewan. University of Saskatchewan, Saskatoon, Saskatchewan.

Matthew, W. D. 1903. The fauna of the *Titanotherium* beds at Pipestone Springs, Montana. Bulletin of the American Museum of Natural History 19:197-226.

Matthew, W. D. 1909. Faunal lists of the Tertiary Mammalia of the West. U.S. Geological Survey Bulletin 361:91-120.

Matthew, W. D. 1910. On the skull of *Apternodus* and the skeleton of a new artiodactyl. Bulletin of the American Museum of Natural History 28:33-42.

McConnell, R. G. 1885. Report on the Cypress Hills, Wood Mountain, and adjacent country: embracing that portion of the district of Assiniboia, lying between the international boundary and the 51st parallell and extending from long. 106 to lon. 10050'. Geological Surveyof Canada, Annual Report, New Series 2 (Part C). Dawson, Montreal, Quebec, 85 pp.

McDougall, Frank H. 1995. A research proposal for a doctoral degree program in vertebrate paleontology. PhD Evaluation of Research Potential, Department of Geological Sciences, University of Saskatchewan, 25 pp.

McDowell, S.B., Jr. 1958. The Greater Antillean insectivores. Bulletin of the American Museum of Natural History 115(3):113–214.

McKenna, M. C. 1960. The Geolabidinae, a new subfamily of Early Cenozoic erinaceoid insectivores. University of California Publications in Geological Science 37:131-164.

McKenna, M. C. 1963. Primitive Paleocene and Eocene Apatemyidae (Mammalia, Insectivora) and the Primate-Insectivore Boundary. American Museum Novitates 2160:1-40.

McKenna, M. C. 1975. Toward a Phylogenetic Classification of the Mammalia; pp. 21-46 in W. P. Luckett and F. S. Szalay (eds.), *Phylogeny of the Primates; a multidisciplinary approach.* Plenum Press, New York, New York.

McKenna, M. C. and S. K. Bell. 1997. A classification of Mammals above the species level. Columbia Univserity Press, New York, New York, 631 pp.

McLearn, F. H. 1928. Stratigraphy, structure, and clay deposits of Eastend area, Cypress Hills, Saskatchewan. Geological Survey of Canada Summary Report for 1927, part B: 21-53.

Meehan, T. J. 2007. Personal communication regarding "*Frictops emryi*".

Meyer, Taran E. 2003. Aplodontidae (Mammalia: Rodentia) and Pteromyindae (Rodentia: Sciuridae) Fauna of the Fossil Bush Locality (Early Oligocene) of the Cypress Hills (Southwest Saskatchewan, Canada). Undergraduate thesis in Paleobiology, University of Saskatchewan, Saskatoon, Saskatchewan 54 pp.

Mouchaty, S. K., A. Gullberg, A. Janke, and U. Arnason. 2000. The phylogenetic position of the Talpidae within Eutheria based on analysis of complete mitochondrial sequences. Molecular and Biological Evolution 17(1): 60-67.

Novacek, M. J. 1976. Early Tertiary vertebrate faunas, Vieja Group, Trans-Pecos, Texas: Insectivora. The Peace-Sellards Series 23:1-18.

Novacek, Michae J. and R. D. E. MacPhee. 1993. Definition and Relationships of Lipotyphla; pp. 13-31 in F. S. Szalay, M. J. Novacek, and M. C. McKenna (eds.), Mammal Phylogeny vol. 2: the Placentals. Springer-Verlag, New York,.

Nurkowski, J. R. 1984. Coal quality, coal rank variation, and its relation to reconstructed overburden, Upper Cretaceous and Tertiary Plains coals, Alberta, Canada. American Association of Petroleum Geologists Bulletin 68:285-295.

Ostrander, G. E. 1983. New Early Oligocene (Chadronian) mammals from the Raben Ranch Local Fauna, Northwest Nebraska. Journal of Paleontology 57(1):128-139.

Ostrander, G. E. 1987. The Early Oligocene (Chadronian) Raben Ranch local fauna, Northwest Nebraska; Marsupialia, Insectivora, Dermoptera, Chiroptera, and Primates; pp. 92-104 in J. E. Martin and G. E. Ostrander (eds.), Papers in Vertebrate paleontology in honor of Morton Green. Museum of Geology, South Dakota School of Mines and Technology, Rapid City, South Dakota.

Patterson, B., and P. O. McGrew. 1937. A soricid and two Erinaceids from the White River Oligocene. Geological Series of Field Museum of Natural History 6(18):245-272.

Prothero, D. R. 1998. The chronological, climatic, and paleogeographic background to North American mammalian evolution; pp. 9-36 in C. M. Janis, K. M. Scott, and L. L. Jacobs (eds.), Evolution of Tertiary Mammals. Cambridge University Press, Cambridge, England.

Prothero, D. R., and R. J. Emry. 1996. Summary; pp. 664-683 in D. R. Prothero and R. J. Emry (eds.), The Terrestrial Eocene-Oligocene transition in North America. Cambridge University Press, Cambridge, England.

Prothero, D. R., and R. J. Emry. 2004. The Chadronian, Orellan, and Whitneyan Land Mammal Ages; pp. 156-168 in M. O. Woodburne (ed.), Late Cretaceous and Cenozoic Mammals of North America. Columbia University Press, New York, New York.

Prothero, D. R., and C. C. Swisher. 1992. Magnetostratigraphy and geochronology of the terrestrial Eocene-Oligocene transition in North America; pp 46-73 in D. R. Prothero and W. A. Bergren (eds.), Eocene-Oligocene Climatic and Biotic Evolution. Princeton University Press, Princeton, New Jersey.

Reed, C. A. 1954. Some fossorial mammals from the Tertiary of western North America. Journal of Paleontology 28(1):102-111.

Reed, C. A., and W. D. Turnbull. 1965. The Mammalian genera *Arctoryctes* and *Cryptoryctes* from the Oligocene and Miocene of North America. Fieldiana Geology 15(2):99-170.

Reed, K. M. 1961. The Proscalopinae, a new Subfamily of Talpid Insectivores. Bulletin of the Museum of Comparative Zoology at Harvard College 125(14):473-494

Repenning, C. A. 1967. Subfamilies and genera of the Soricidae. U. S. Geological Survey Professional Paper, 74 pp.

Romer, A. S. 1945. Vertebrate paleontology. University of Chicago Press, Chicago, Illinois, 687 pp.

Romer, A. S. 1966. Vertebrate paleontology, 3rd Edition. University of Chicago Press, Chicago, Illinois, 468 pp.

Rothecker, Jennifer M. 2003. The Eomyidae and Cricetidae of the Rodent Hill Local Fauna, Cypress Hills Formation, Saskatchewan. M. S. Thesis, University of Saskatchewan, Saskatoon, Saskatchewan, 135 pp.

Russell, Dale A. 1960. A review of the Oligocene insectivore *Micropternodus borealis*. Journal of Paleontology 34(5):940-949.

Russell, D. E., M. Godinot, P. Louis, and D. E. Savage. 1979. Apatotheria (Mammalia) de l'Eocène inférieur de France et de Belgique. Bulletin du Muséum National d'Histoire Naturelle, section C: Science de la Terre 1(3):203-243.

Russell, L. S. 1934. Revision of the Lower Oligocene vertebrate fauna of the Cypress Hills, Saskatchewan. Proceedings and Transactions of the Royal Canadian Institute 1:49-67.

Russell, L. S. 1936. New and interesting mammalian fossils from Western Canada. Proceedings and Transactions of the Royal Society of Canada, Series 3 30(section 4): 75-80.

Russell, L. S. 1938. The skull of *Hemipsalodon grandis*, a giant Oligocene creodont. Proceedings and Transactions of the Royal Society of Canada, Series 3 32(section 4): 61-65.

Russell, L. S. 1940. Titanotheres from the Lower Oligocene Cypress Hills Formation of Saskatchewan. Proceedings and Transactions of the Royal Society of Canada, Series 3 34(section 4) 89-100.

Russell, L. S. 1950.The Tertiary gravels of Saskatchewan. Proceedings and Transactions of the Royal Society of Canada, Series 3 44(section 4):51-59.

Russell, L. S. 1957. Tertiary plains of Alberta and Saskatchewan. Proceedings of the Geological Association of Canada 9:17-19.

Russell, L. S. 1965. Tertiary mammals of Saskatchewan Part I: The Eocene fauna. Life Sciences Contributions, Royal Ontario Museum 67:1-97.

Russell, L. S. 1972. Tertiary Mammals of Saskatchewan Part II: The Oligocene Fauna, Non-Ungulate Orders. Life Sciences Contributions, Royal Ontario Museum 84:1-97.

Russell, L. S. 1975. Revision of the fossil horses from the Cypress Hills Formation (Lower Oligocene) of Saskatchewan. Canadian Journal of Earth Sciences 12(4): 636-648

Russell, L. S. 1978. Tertiary mammals of Saskatchewan. Part IV: the Oligocene anthracotheres. Life Science Contributions, Royal Ontario Museum 122:1-58.

Russell, L. S. 1980a. Tertiary Mammals of Saskatchewan Part V: The Oligocene Entelodonts. Life Sciences Contributions, Royal Ontario Museum 122: 1-42.

Russell, L. S. 1980b. A new speciesof *Brachyhyops?* (Mammalia, Artiodactyla) from the Oligocene Cypress Hills Formation of Saskatchewan. Life Sciences Occasional Papers, Royal Ontario Museum 33:1-5.

Russell, L. S. 1982. Tertiary mammals of Saskatchewan Part VI: the Oligocene rhinoceroses. Life Sciences Contributions, Royal Ontario Museum 133: 1-58.

Russell, L. S. 1984. Tertiary mammals of Saskatchewan. Part VII: Oligocene marsupials. Life Sciences Contributions, Royal Ontario Museum 139: 1-12.

Russell, L. S., and R. T. D. Wickenden. 1933. An upper Eocene vertebrate fauna from Saskatchewan. Proceedings and Transactions of the Royal Society of Canada, Series 3 27(section 4):53-65.

Schlaikjer, E. M. 1934. A new fossil zalamdodont insectivore. American Museum Novitates 698:1-8.

Schlaikjer, E. M. 1935. Contributions to the stratigraphy and paleontology of the Goshen Hole Area, Wyoming; 1, a detailed study of the structure and relationships of a new zalamdodont insectivore from the middle Oligocene. Bulletin of the Museum of Comparative Zoology at Harvard College 76(1):33-68.

Scott, William Berryman and Glenn Lowell Jepsen. 1936. The mammalian fauna of the White River Oligocene. Transactions of the American Philosophical Society

(New Series), 28:iii-151
Skwara, T. 1986. A new "flying squirrel" from the Early Miocene of southwestern Saskatchewan. Journal of Vertebrate Paleontology, 6:290-294
Skwara, T. 1988. Mammals of the Topham local fauna: Early Miocene (Hemingfordian), Cypress Hills Formation, Saskatchewan. Natural History Contributions, Saskatchewan Museum of Natural History 9. Regina, Saskatchewan,169 pp.
Simpson, G. G. 1941. A new Oligocene insectivore. American Museum Novitates 1150:1-3
Simpson, G. G. 1945. The principles of classification and the classification of mammals. Bulletin of the American Museum of Natural History 85: 14-350.
Springer, M. S., G. C., Cleven, O. Madsen, W. W. de Jong, V. G. Waddell, H. M. Amrine, and M. J. Stanhope. 1997. Endemic African mammals shake the phylogenetic tree. Nature 388: 61-64.
Stanhope, M. J., V.G. Waddell, O. Madwen, W. de Jong, S. B. Hedges, G. C. Cleven, D. Kao, and M. S. Springer. 1998. Molecular evidence for multiple origins of Insectivora and for a new order of endemic African insectivore mammals. Proceedings of the National Academy of Sciences USA 95: 9967-9972.
Sternberg, C. M. 1924. Notes on the Lance Formation of southern Saskatchewan. The Canadian Field-Naturalist 38: 66-70.
Stirton, R. A., and J. M. Rensberger. 1964. Occurrence of the insectivore genus *Micropternodus* in the John Day Formation of central Oregon. Bulletin of the Southern California Academy of Sciences 63(2):57-80.
Stock, C. 1949. Mammalian fauna from the Titus Canyon Formation, California. Carnegie Institution of Washington Publications, Contributions to Paleontology 584: 229-244.
Storer, J. E. 1975a. Middle Miocene Mammals from the Cypress Hills, Canada. Canadian Journal of Earth Sciences 12(3): 520-522
Storer, J. E. 1975b. Tertiary mammals of Saskatchewan. Part III: the Miocene Fauna. Life Science Contributions, Royal Ontario Museum, 103: 1-134.
Storer, J. E. 1978. Rodents of the Calf Creek Local Fauna (Cypress Hills Formation, Oligocene, Chadronian), Saskatchewan. Natural History Contributions, Saskatchewan Museum of Natural History 1: 1-54.
Storer, J. E. 1981a. Leptomerycid Artiodactyla of the Calf Creek Local Faunna (Cypress Hills Formation, Oligocene, Chadronian), Saskatchewan. Natural History Contributions, Saskatchewan Museum of Natural History 3: 1-32.
Storer, J. E. 1981b. Lagomorphs of the Calf Creek Local Fauna (Cypress HIlls Formation, Oligocene, Chadronian), Saskatchewan. Natural History Contributions, Saskatchewan Museum of Natural History 4: 1-14.
Storer, J. E. 1983. A new species of the artiodactyl *Heptacodon* from the Cypress Hills Formation, Lac Pelletier, Saskatchewan. Canadian Journal of Earth Sciences, 20: 1344-1347.
Storer, J. E. 1984a. Fossil mammals of the Southfork Local Fauna (Early Chadronian) of Saskatchewan. Canadian Journal of Earth Sciences 21:1400-1405.
Storer, J. E. 1984b. Mammals of the Swift Current Creek Local Fauna (Eocene: Uintan), Saskatchewan. Natural History Contributions, Saskatchewan Museum of Natural History 7: 1-58.

Storer, J. E. 1987. Dental evolution and radiation of Eocene and Early Oligocene Eomyidae (Mammalia:Rodentia) of North America, with new material from the Duchesnean of Saskatchewan. *Dakoterra,* 3: 108-117.

Storer, J. E. 1988. The rodents of the Lac Pelletier Lower Fauna, Late Eocene (Duchesnean) of Saskatchewan. Journal of Vertebrate Paleontology 8: 84-101.

Storer, J. E. 1990. Primates of the Lac Pelletier Lower Fauna (Eocene: Duchesnean), Saskatchewan. Canadian Journal of Earth Sciences 27: 17-29.

Storer, J. E. 1992. *Tachylagus*, a new lagomorph from the Lac Pelletier Lower Fauna (Eocene: Duchesnean) of Saskatchewan. Journal of Vertebrate Paleontology 12: 230-235.

Storer, J. E. 1993a. Multituberculates of the Lac Pelletier Lower Fauna, Late Eocene (Duchesnean), of Saskatchewan. Canadian Journal of Earth Sciences 30: 1613-1617.

Storer, J. E. 1993b. Additions to the mammalian paleofauna of Saskatchewan. Modern Geology 18:475-487.

Storer, J. E. 1993c. Letter to Kevin Seymour, Department of Vertebrate Paleontology, Royal Ontario Museum, 2 pp.

Storer, J. E. 1994. A latest Chadronian (Late Eocene) mammalian fauna from the Cypress Hills, Saskatchewan. Canadian Journal of Earth Sciences 31: 1335-1341.

Storer, J. E. 1995. Small mammals of the Lac Pelletier Lower Fauna, Duchesnean, of Saskatchewan, Canada: insectivores and insectivore-like groups, a plagiomenid, a microsyopid, and chiroptera; pp. 595-615 in W. A. S. Sarjeant (ed.), Vertebrate fossils and the evolution of scientific concepts. Godon and Breach, Amsterdam, Netherlands.

Storer, J. E. 1996. Eocene-Oligocene Faunas of the Cypress Hills Formation, Saskatchewan; pp. 240-261 in D. R. Prothero and R. J. Emry (eds.), The Terrestrial Eocene-Oligocene transition in North America. Cambridge University Press, New York, New York.

Storer, J. E. 2002. Small mammals of the Kealey Springs Local Fauna (Early Arikareean; Late Oligocene) of Saskatchewan. Paludicola 3(4): 105-133.

Storer, J. E. and H. N. Bryant. 1993. Biostratigraphy of the Cypress Hills Formation (Eocene to Miocene), Saskatchewan: equid types (Mammalia: Perissodactyla) and associated faunal assemblages. Journal of Paleontology 67(4):660-669.

Storer, J. E. and H. N. Bryant. 1997. Tertiary mammal faunas of the Cypress Hills Formation, Southwestern Saskatchewan; pp. 112-122 in Canadian Paleontology Conference Field Trip Guidebook No. 6. Upper Cretaceous and Tertiary Stratigraphy and Paleontology of Southern Saskatchewan. Geological Association of Canada.

Stirton, R. A., and J. M. Rensberger. 1964. Occurrence of the insectivore genus *Micropternodus* in the John Day Formation of central Oregon. Bulletin of the Southern California Academy of Sciences 63(2):57-80.

Tabrum, A. R., and R. W. Fields. 1980. Revised Mammalian faunal list for the Pipestone Springs Local Fauna (Chadronian, Early Oligocene), Jefferson Country, Montana. Northwest Geology, 9:45-51.

Tabrum, A. R., D. R. Prothero, and D. Garcia. 1996. Magnetostratigraphy and biostratigraphy of the Eocene-Oligocene transition, southwestern Montana; pp.

278-311 in D.R. Prothero and R. J. Emry (eds.), the Terrestrial Eocene-Oligocene transition in North America. Cambridge University Press, New York, New York.

Tabrum, A. R., R. Nichols, A. D. Barnosky. 2001. Tertiary Paleontology of Southwest Montana and adjacent Idaho. Guidebook to Field Trips, Society of Vertebrate Paleontology 61st Annual Meeting, Mesozoic and Cenozoic Paleontology inthe Western Plains and Rocky Mountains. Museum of the Rockies Occasional Paper 3: 93-112.

Trouessart, E.-L. 1879. Catalogus Mammalium tam viventium quam fossilium. Nova editio: Berolinhi, R. Friedlander & Sohn, fasc. 1-3, 8 volumes, pp. 665-1264.

Van Valen, L. 1967. New Paleocene insectivores and insectivore classification. Bulletin of the American Museum of Natural History 135(5):217-284.

Vonhof, J. A. 1965. Tertiary sands and gravel in southern Saskatchewan. M. S. thesis, University of Saskatchewan, Saskatoon, Saskatchewan, 99 pp.

Vonhof, J. A. 1969. Tertiary gravels and sands in the Canadian Great Plains. Ph.D. thesis, University of Saskatchewan, 170 pp.

Waddell, P. J., N. Okada, and M. Hasegawa. 1999. Towards resolving the interordinal relationships of placental mammals. Systematic Biology 48(1):1-5.

Weigel, R. D. 1963. Oligocene birds from Saskatchewan. Florida Scientist 26(3):257-262.

West, R. M. 1972. Upper deciduous dentition of the Oligocene insectivore *Leptictis (=Ictops) actutidens.* Annals of Carnegie Museum 44(3):25-32.

West, R. M., and E. G. Atkins. 1970. Additional Middle Eocene (Bridgerian) Mammals from Tavernacle Butte, Sublette Country, Wyoming. American Museum Novitates 2404:1-26.

Weston, T. C. 1894. Notes on the Miocene Tertiary rocks of the Cypress Hills, North-West Territory of Canada. Proceedings and Transactions of the Nova Scotian Institute of Science 8 (2nd series vol. 1):223-227.

Whidden, H. P. 2002. Extrinsic snouth musculature in Afrotheria and Lipotyphla. Journal of Mammalian Evolution 9(1/2): 161-184.

White, Theodore E. 1954. Preliminary analysis of the fossil vertebrates of the Canyon Ferry Area. Proceedings of the U.S. National Museum 103(3326): 395-437.

Williams, M. Y., and W. S. Dyer. 1930. Geology of Southern Alberta and Southwestern Saskatchewan. Geological Survey of Canada Memoirs 163: 1-160.

Williams, M. R., and J. E. Storer. 1998. Cricetid rodents of the Kealey Springs local fauna (Early Arikareean: Late Oligocene) of Saskatchewan. Paludicola 1(4): 143-149.

Wilson, John A. 1986. Stratigraphic occurrence and correlation of early Tertiary vertebrate faunas, Trans-Pecos Texas: Agua Fria-Green Valley areas. Journal of Vertebrate Paleontology 6(4):250-375.

Wood, H. E., R. W. Chaney, J. Clar, E. H. Colbert, G. L. Jepsen, J. B. Reeside, Jr., C. Stock. 1941. Nomenclature and Correlation of the North American Continental Tertiary. Bulletin of the Geological Society of America 52:1-48

Plate I (*Apternodus*)

A, LP4 P661.479, occlusal view
B, LM1 ROM 23254, occlusal view
C, LM1 ROM 23254, anterior view
D, RM3 P2187.275, occlusal view
E, Lp2? P2113.885, occlusal view
F, Lp2? P2113.885, lingual view
G, Rm1 or 2 P2187.277, occlusal view
H, Rm1 or 2 P2187.277, buccal view
I, Rm3 P2113.719, occlusal view

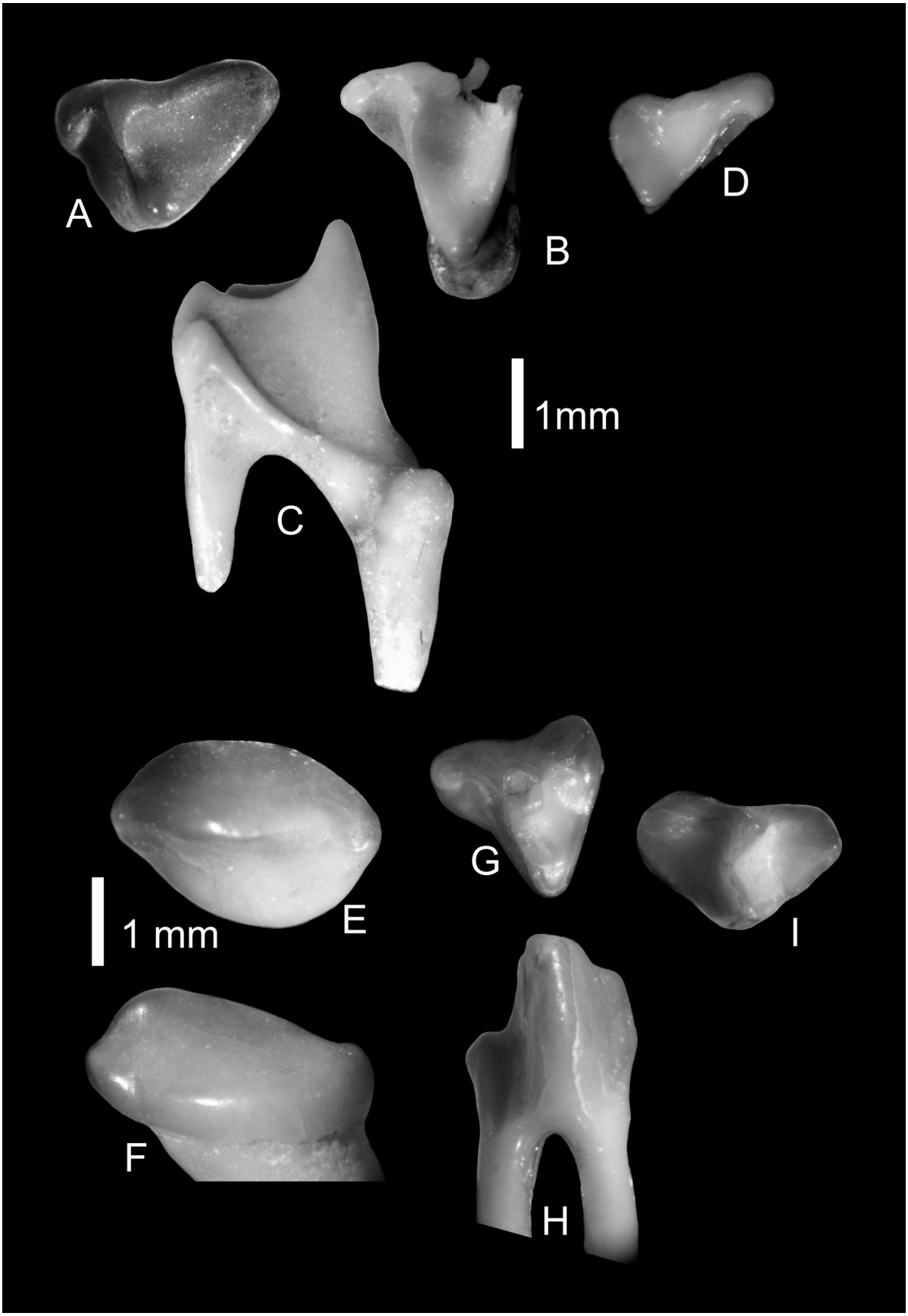

A
B
D
C
1mm
G
E
1 mm
I
F
H

Plate II (*Centetodon chadronensis*)

A, RP3 P1585.959, occlusal view
B, LP4 P1585.958, occlusal view
C, RM1 P1585.965, occlusal view (reversed; see Fig. 4.3)
D, RM2 P1585.969, occlusal view (reversed)
E, RM3 P1585.970, occlusal view (reversed)
F, RP3 P1585.959, buccal view
G, LP4 P1585.958, posterior view
H, RM1 P1585.965, lingual view
I, LM1 ROM 23251, lingual view
J, Lm1 or 2 P2113.677, occlusal view (see Fig. 4.4)
K, Lm3 P2113.676, occlusal view
L, Lm1 or 2 P2113.677, buccal view

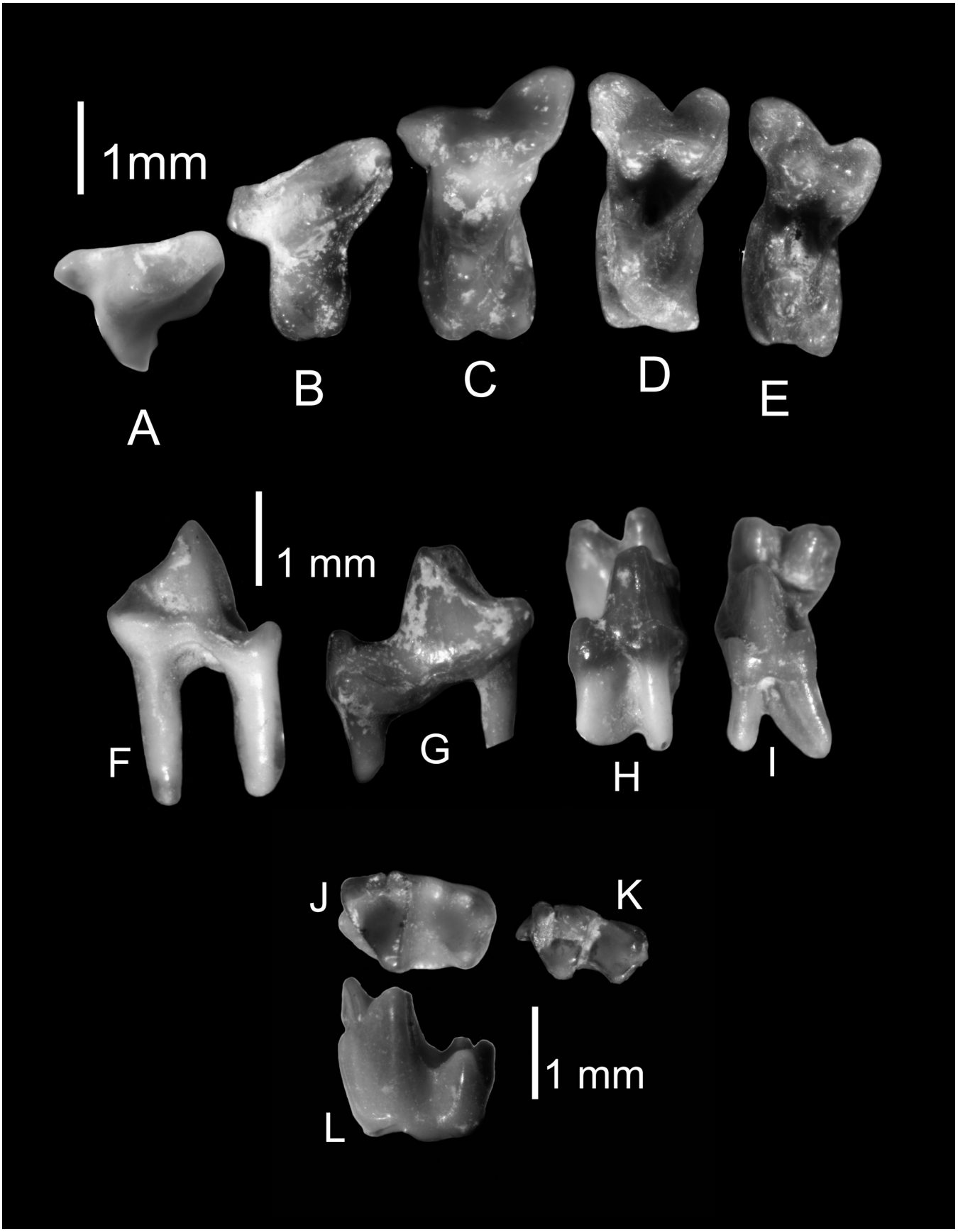
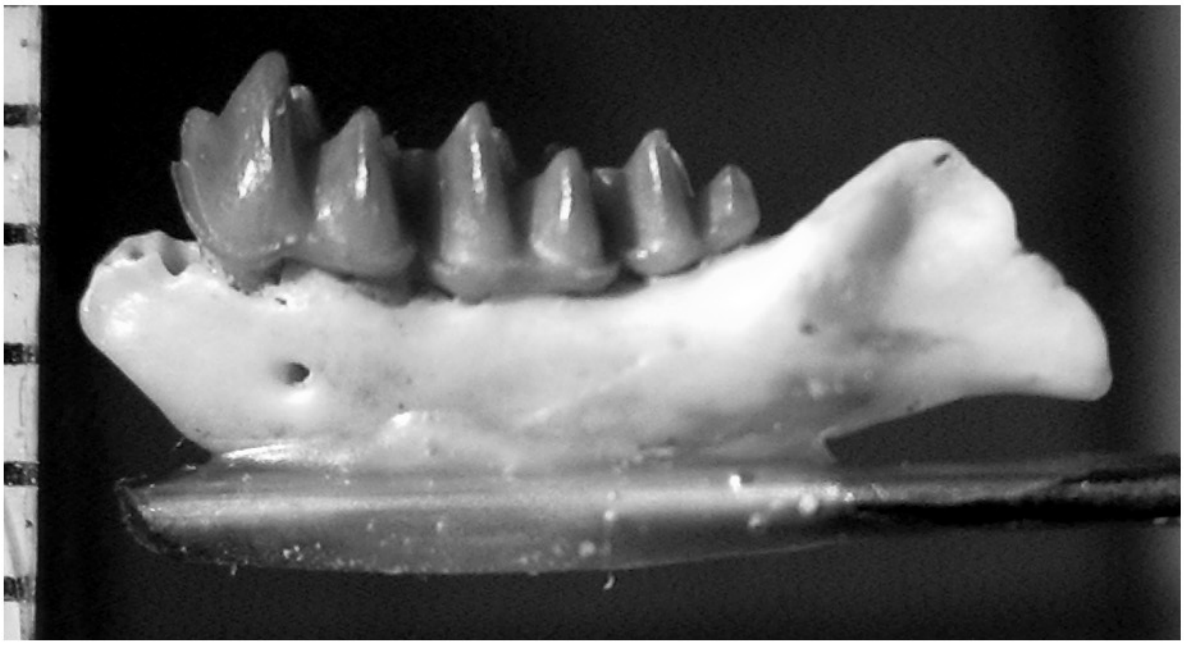

1mm
A
B
C
D
E
1 mm
F
G
H
I
J
K
1 mm
L

Plate III (*Domnina thompsoni*)

A, P2431.005, buccal view
B, P2431.005, lingual view

A



B

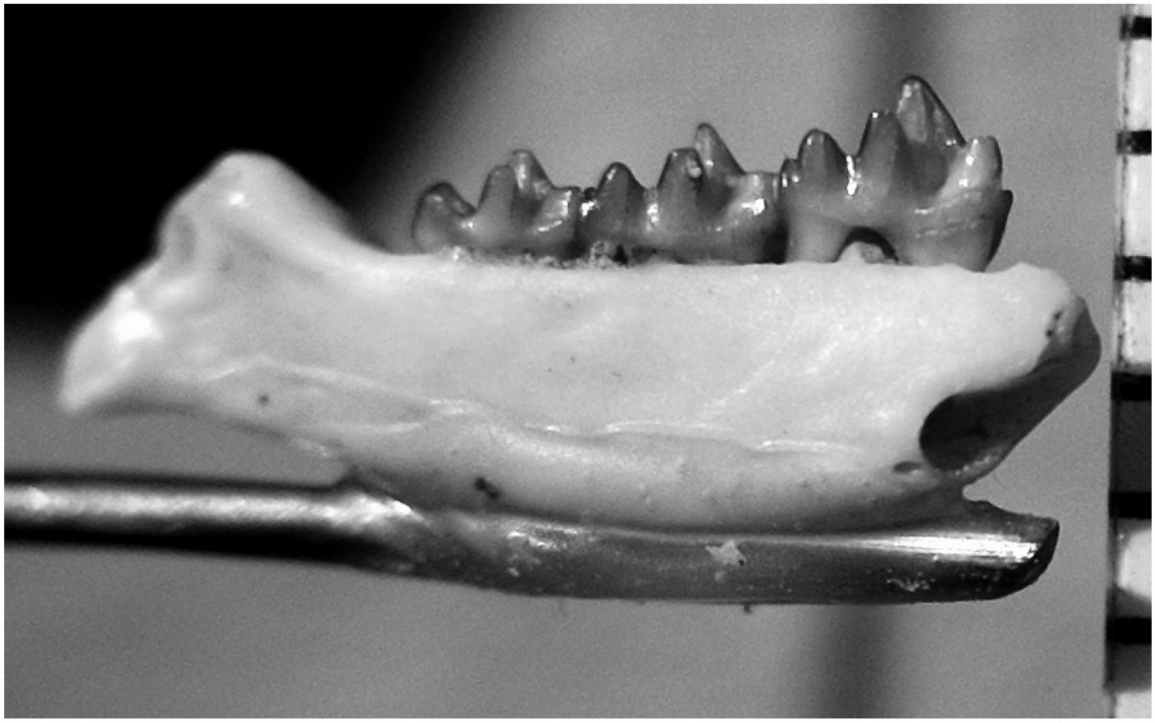


Plate IV (*Micropternodus strophensis*)

A, RP4 P2113.735, buccal view
B, RP4 P2113.735, posterior view
C, Rp4 P2113.776, buccal view (reversed)
D, Lm1 P2113.728, occlusal view
E, Lm2 P1585.949, occlusal view
F, Rm3 1585.954, occlusal view (reversed)
G, Rp4 P2113.776, lingual view (reversed)
H, Lm1 P2113.728, anterior view
I, Lm2 P1585.949, buccal view
J, Rm3, 1585.954, buccal view (reversed)

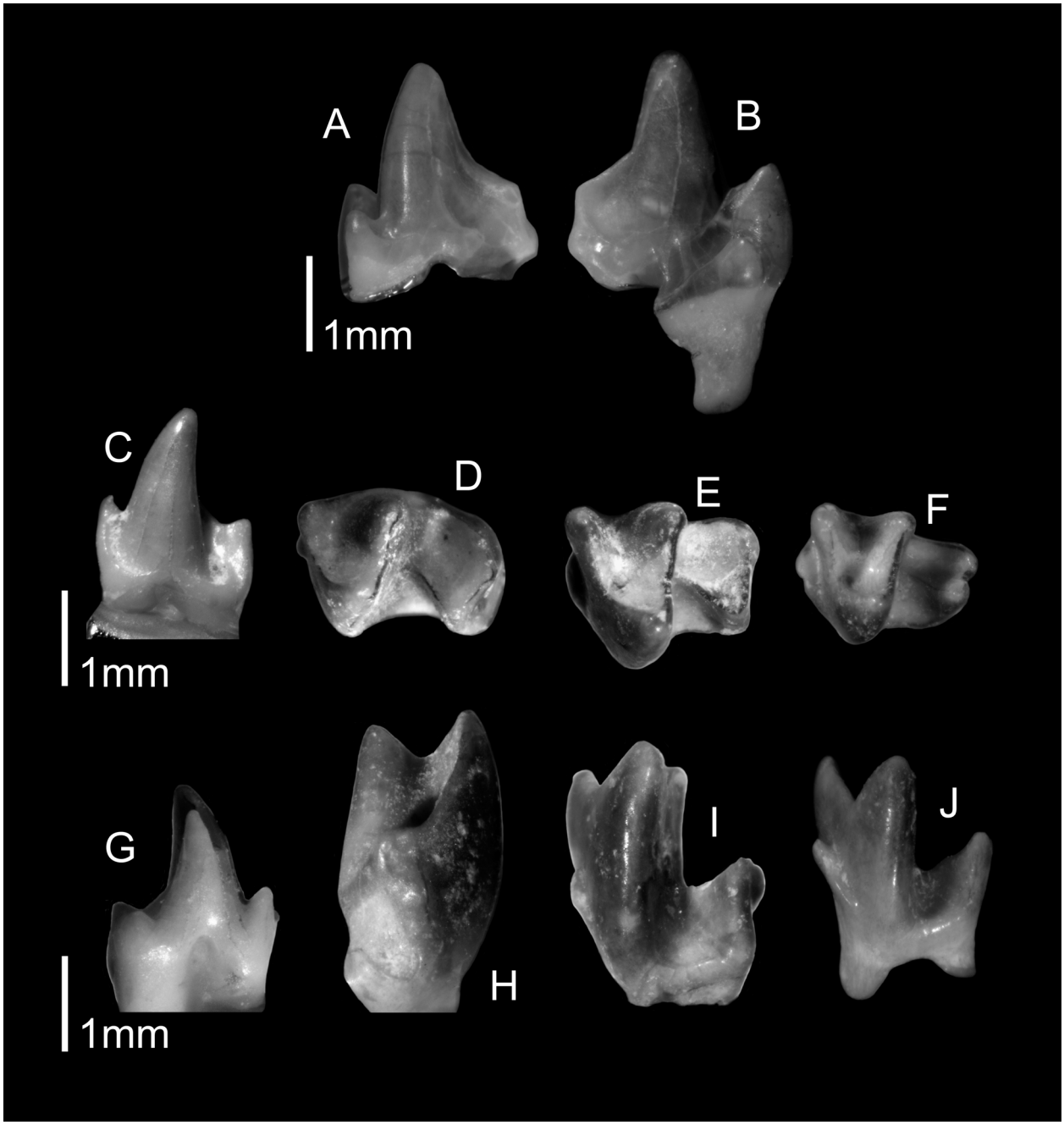

A
B
1mm
C
D
E
F
1mm
G
H
I
J
1mm

Plate V (*Micropternodus* cf. *M. montrosensis* and *Oligoryctes altitalonidus*)

A, RM2 P1585.941, *Micropternpodus* cf. *M. montrosensis*, occlusal view
B, RP4 or M1 P2113.778, *Oligoryctes altitalonidus*, anterior view
C, RP4 or M1 P2113.778, *Oligoryctes altitalonidus,* occlusal view
D, left mandible fragment with Lm1 to 3 P2187.271, *Oligoryctes altitalonidus,* buccal view
E, mandible fragment with Lm1 to 3 P2187.271, *Oligoryctes altitalonidus,* lingual view
F, left mandible fragment with coronoid process and mandibular condyle P661.489, *Oligoryctes altitalonidus,* lingual view

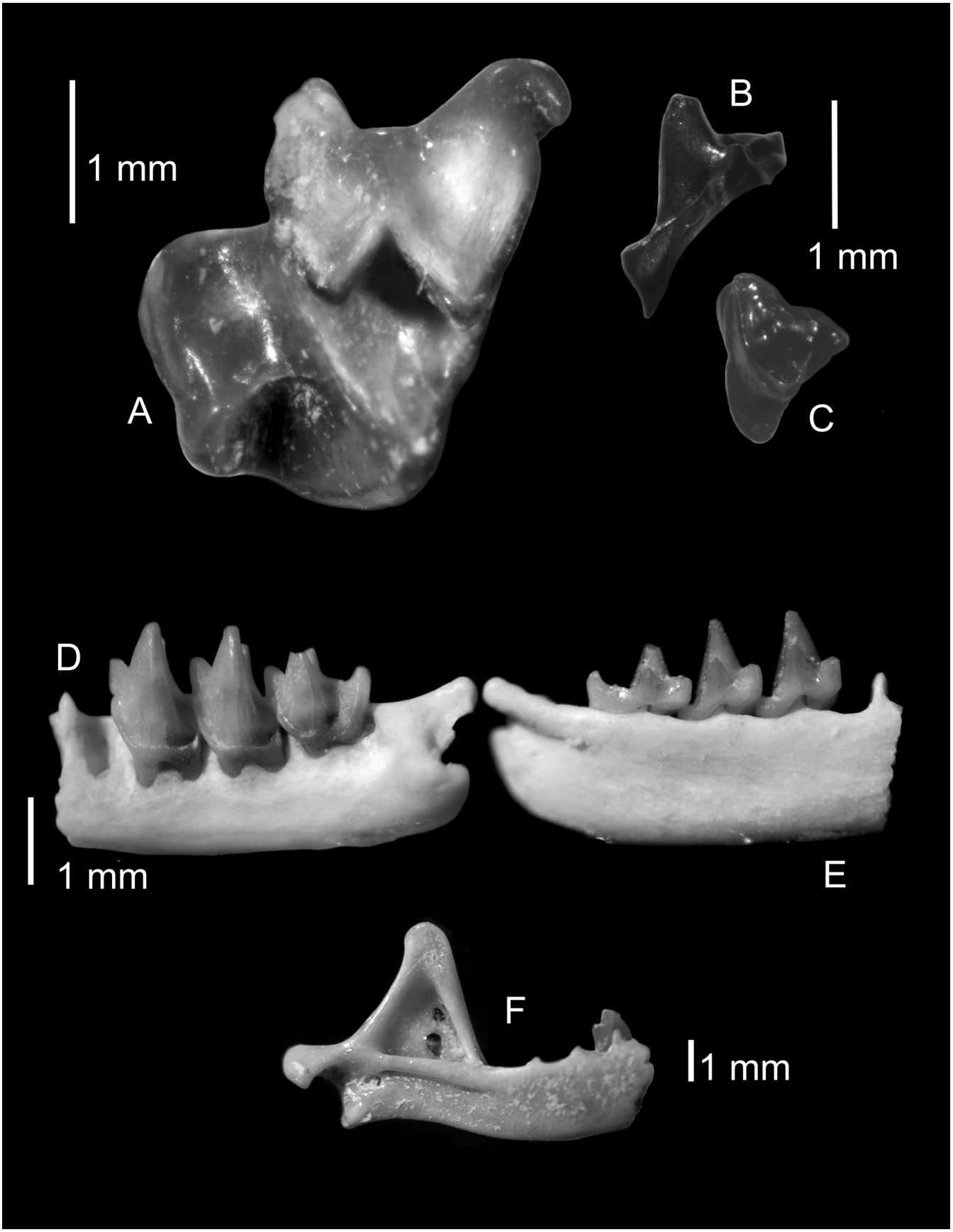

1 mm
A
B
1 mm
C
D
1 mm
E
F
1 mm

Plate VI (*Sinclairella*)

A, LM2 P661.496, occlusal view
B, Lm1 P1585.981, occlusal view
C, Lm2 ROM 23256, occlusal view
D, Lm3 ROM 44357, occlusal view

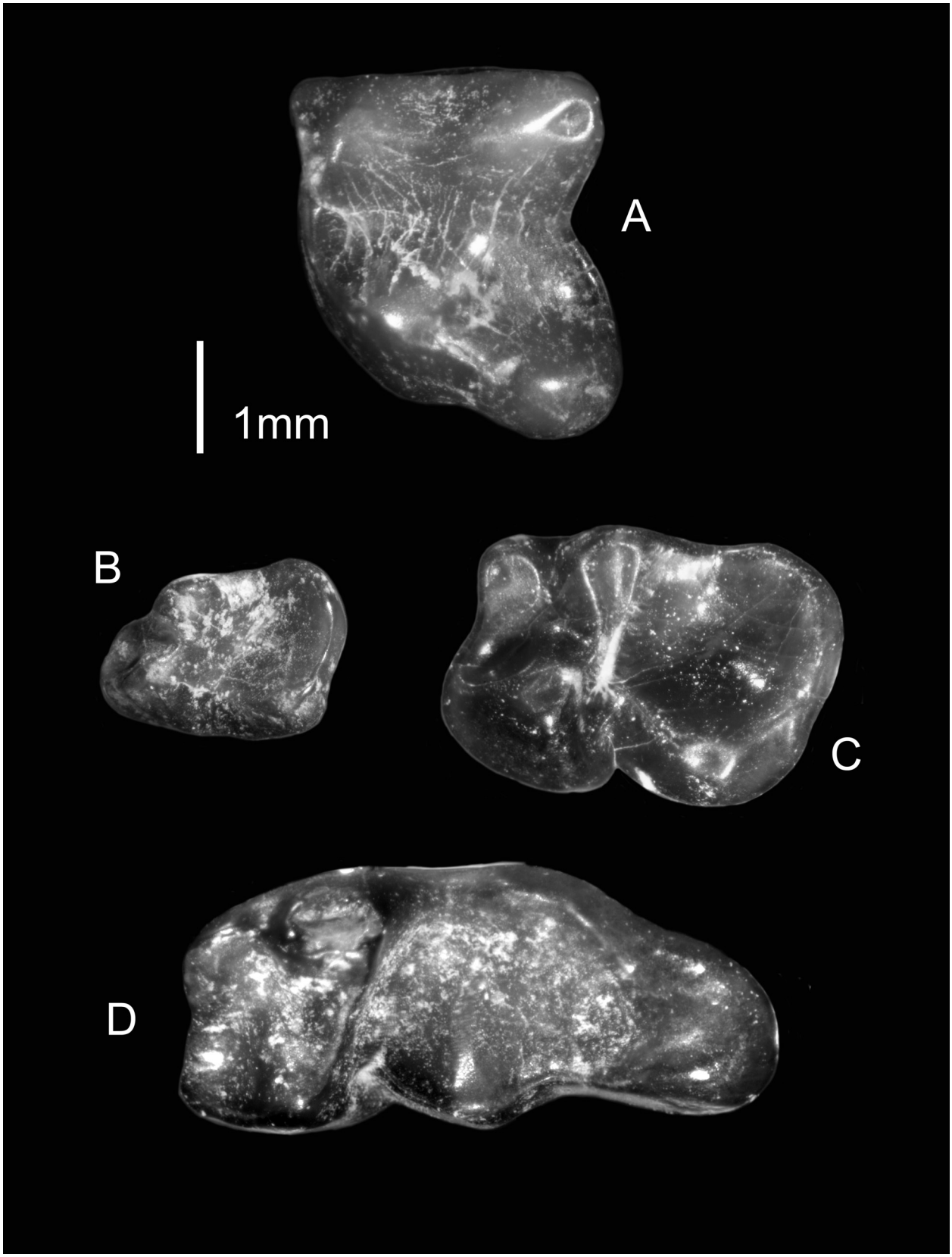

A
1mm
B
C
D

Plate VII (*Leptictis acutidens*)

A, LDP3 P661.2125, occlusal view
B, RP3 ROM 44356, occlusal view (anterior to right)
C, LP4 P2187.245, occlusal view
D, LDP3 P661.2125, buccal view (anterior to right)
E, RP3 ROM 44356, lingual view (anterior to right)
F, LM1 or 2 P2483.009, occlusal view
G, LM1 or 2 ROM 6243, occlusal view
H, RM3 P1585.911, occlusal view (shown reversed)
I, Rm3 P661.473, occlusal view (anterior to right)
J, Rm1 or 2 P2187.278, occlusal view (anterior to right)
K, Rp4 P2113.003, occlusal view (anterior to right)

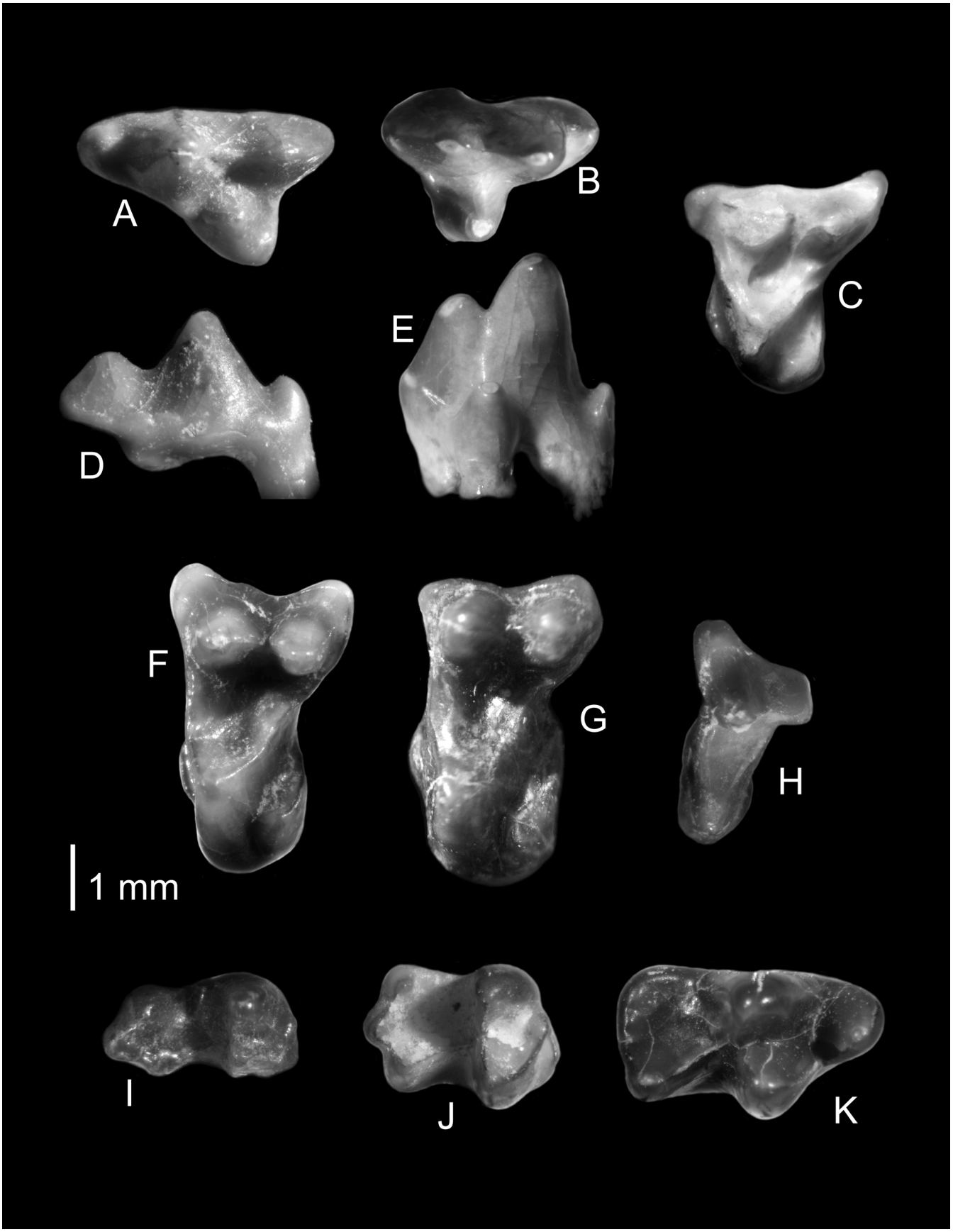
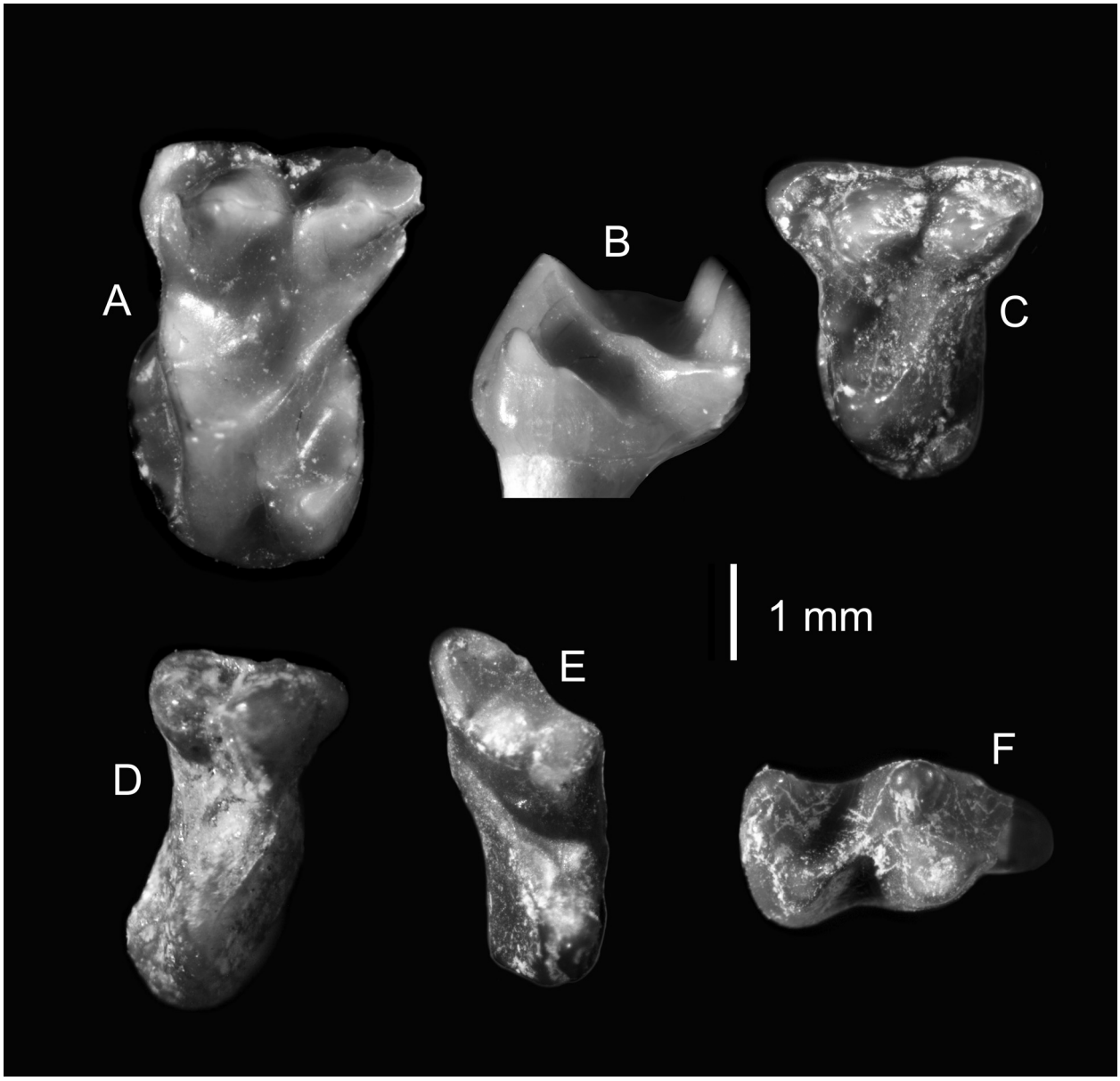

A
B
C
D
E
F
G
H
1 mm
I
J
K

Plate VIII (*Leptictis wilsoni* and *Leptictis thomsoni*)

A, LM1 or 2 P2113.002, *Leptictis wilsoni,* occlusal view
B, LM1 or 2 P2113.002, *Leptictis wilsoni,* posterior view of lingual portion
C, LP4 P661.2124, *Leptictis wilsoni,* occlusal view
D, RM1 or 2 P661.467, *Leptictis thomsoni,* occlusal view (anterior to right)
E, RM1 or 2 P1585.907, *Leptictis ?thomsoni,* occlusal view (anterior to right)
F, Rp4 P1585.984, *Leptictis ?thomsoni,* occlusal view (anterior to right)


A
B
C
1 mm
D
E
F